#90

NOAA Technical Report NMFS 90

August 1990

Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries

Harold L. Pratt, Jr.
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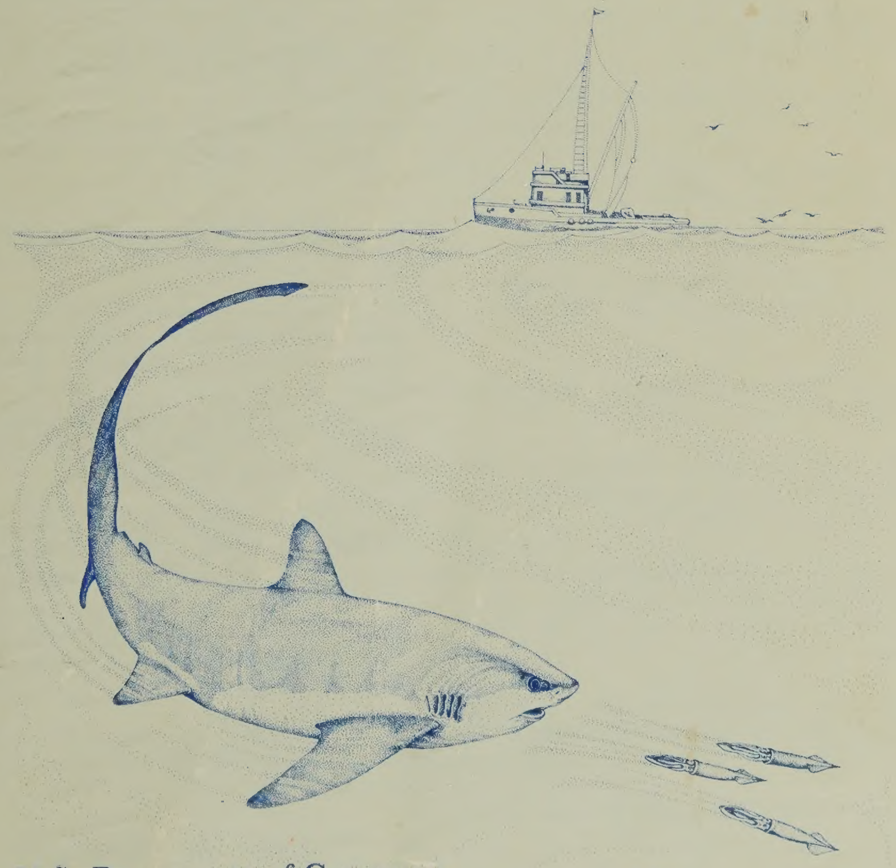

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Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries

Proceedings of the Second United States–Japan Workshop
East-West Center, Honolulu, Hawaii
9–14 December 1987

Harold L. Pratt, Jr.
Samuel H. Gruber
Toru Taniuchi (editors)

Sponsored by:
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August 1990

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PREFACE

This report owes its genesis to the foresight and enthusiam of Dr. Kazuhiro Mizue. By happy circumstance, Professor Mizue contacted me in 1983 with his visionary ideas on cooperative programs. He noted that the time was right because the Japan Society for the Promotion of Science and the National Science Foundation had mutually given priority to cooperative programs in marine biology.

I therefore agreed to act as the U.S. coordinator and proposed to NSF, a short trip to Japan to negotiate site visits and timing with ten previously appointed Japanese scientists and, if that trip were successful, to negotiate a joint research project, possibly followed by a joint seminar.

The success of that trip and subsequent funding of the joint seminar and project were due in large part to coordination by my wife Mariko, who speaks Japanese and who made the many office hours of difficult meetings bearable; to Dr. Toru Taniuchi, who kept up a stream of useful information, both social and administrative; and to Dr. Charles Wallace of NSF, who encouraged me from the beginning. Mention should also be given to Dr. Charles Owen of the U.S. Embassy in Tokyo, who helped us through the considerable red tape of international programs in the host country.

After a productive first meeting, during which most of the 13 U.S. and Japanese scientists presented their results at the Second Indo-Pacific Fish Conference in Uyeno, Tokyo, it was decided that we should proceed with a comprehensive joint seminar on chondrichthyan fishery biology. By then, Professor Mizue had retired and Dr. Mikio Oguri became the Japanese principal investigator.

The smooth, efficient staging of four days of meetings was due in large part to James McMahon and his competent staff at the University of Hawaii's East-West center. We are all in their debt. Finally, this book would have been only an academician's dream without the efforts of the senior editor who took on the real task of completing it and making it a reality. Thanks Wes!

Samuel H. Gruber
Miami, September 21, 1989

INTRODUCTION

Elasmobranchs have always been important to people dependent on or interested in the sea. They have provided a vast number of products, ranging from food and pharmaceuticals to clothing and novelties. People are fascinated by them. General knowledge and sometimes misinformation about the more dramatic species: stingrays, white and hammerhead sharks, manta rays, and makos, have thrilled and entertained millions of people worldwide.

Studies of their anatomy and systematics have enriched our understanding of other chordate classes, medical science, and the order and structure of taxonomy. Investigations of their ecology and life history help us to understand large marine ecosystems and food webs.

Recently, national interest in shark food products has increased dramatically and a global market has developed. Shark damage to the highly valuable finfish catch is a large financial burden to some countries; consequently many sharks are destroyed. Untold thousands are destroyed as bycatch simply because their economic value is too low for fishermen to keep them. As a result of this multifaceted exploitation and mankind's effects on the environment, elasmobranch stocks are heavily impacted. Conservation and management have not kept pace with utilization. Our knowledge of these important and exciting animals is, and always has been, limited.

The focus of the U.S.–Japan workshop was to address recent advances in elasmobranch research in the hope of providing at least a temporary benchmark and reference work for ourselves, for fellow researchers, for those charged with managing marine resources, and for students of elasmobranch biology. The workshop provided a forum for exchange of ideas and ideologies; and provided both a place at which past joint research projects could be culminated and a point of intersection for new cooperative endeavors.

Fifty-two participants from seven different countries delivered research reports and participated in two workshop sessions. Of the 43 oral papers, 36 were accepted as final manuscripts. Each manuscript was sent to two or three anonymous reviewers. Over 90 reviews were performed by 27 workshop attendees and 39 outside specialists. Japanese and Mexican papers were submitted in English and edited for style, checked by the authors, sent out for peer review with the rest, edited, revised, edited again and double checked by each author.

Manuscripts range in scope from current updates on fisheries landings and trends, both worldwide and local; to evaluations of the unique internal ecology of bacteria in shark tissues. Papers include submersible observations of deep sea sharks and anatomical observations with the superwide field scanning electron microscope. We have tried to create a book that will be worthwhile reading as well as a reference work for many years to come.

Nomenclature follows the American Fisheries Society, Special Publication 12: ''A List of Common and Scientific Names of Fishes from the United States and Canada,'' fourth edition, 1980; and secondarily, the FAO Species Catalogue, Vol. 4, Part 2, ''Sharks of the World,'' by L. J. V. Compagno, 1984.

I would like to thank my co-editors for comments, help and encouragement as the project proceeded: Jack Casey and Ken Sherman for support and advice; Laura Hedrick for her patience and skill in typing and retyping many of the manuscripts, tables, and correspondence; and Steve Branstetter for transcription of the Workshop audiotapes and help over some rough spots. I thank Frank Murru and Mark Nichols of Sea World, Orlando, for cover art work and Rolf Williams for his hard work on our behalf. My sincere appreciation goes to the reviewers whose quiet work substantially changed and improved the manuscripts. I especially thank all of the authors for sharing their research with us. Together you have carried the lamp of knowledge a little closer toward understanding elasmobranch biology.

Harold L. Pratt, Jr., Senior Editor
Narragansett, October 7, 1989

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Life-History Patterns in the Elasmobranchs: Implications for Fisheries Management

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ABSTRACT

The life-history patterns of elasmobranchs are very different from most teleosts and appear to fall in the realm of the so-called "*K*-selected species" of classic *r*/*K* selection theory. The authors explore the connections between life-history studies, *r*/*K* selection theory, and the theory of fisheries management. Considerations of life history and the predictions of *r*/*K* selection theory can provide useful results for fisheries management in two ways: by providing estimates of, and methods for estimating, important life-history parameters and by providing a basis for predicting and ranking the resiliency of species to exploitation. The rate of population increase appears implicitly in stock production models and age-structured (e.g., Leslie matrix) models of fisheries management. Considerations of life history patterns may provide guidance in quantifying the intrinsic rate of increase.

Introduction

Elasmobranchs have been evolving independently for at least 450 million years and, by the Carboniferous period, they seem to have developed a life-history pattern similar to that seen today. This pattern, typically consisting of slow growth, large adult size, late reproduction, and the production of few, well-formed young, is quite different from that typically found in the other great class of fish-like vertebrates, the teleosts. Here the pattern generally seen consists of rapid growth, a relatively short life cycle, and many fragile offspring. Elasmobranchs in essence have evolved a life-history strategy very similar to the marine reptiles and mammals.

Most traditional fishery models developed for teleosts do not assume any direct relationship between stock and recruitment (Ricker 1975), although such a relationship must exist because no fish present implies no recruitment. Highly variable survival of the early life stages of teleosts has long been noted, and environmental conditions during the first year of life appear to play an important role in determining the recruitment of new cohorts into teleost stocks (Rothschild 1986). On the other hand, the relationship between stock and recruitment in the elasmobranchs is quite direct, owing to the reproductive strategy of low fecundity combined with few, well-formed offspring. Although there is some evidence that fecundity of sharks increases as the stocks decline (Holden 1977), in general the number of young that can be produced is strictly limited and dependent on the number of adults in the stock. Thus, unlike the strategy for a cod or flounder fishery, the relationship between parental stock and recruitment success must be of prime consideration in the development of a rational strategy for exploitation of elasmobranch stocks.

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From a practical point of view the life-history pattern of elasmobranchs makes this group of animals extremely susceptible to over fishing. It is no coincidence that the commercially exploited marine turtles and baleen whales, which have life-history patterns similar to the sharks, are also in trouble. Indeed, the strong relationship between parental stock and recruitment in the elasmobranchs has led some to question whether it is possible to have sustained exploitation (Holden 1974). If this question is taken literally, the answer is obviously "yes"—many wild animals, such as the ungulates, have life-history traits similar to those mentioned for the elasmobranchs yet they have supported sustained harvests for centuries. On a deeper level, it is less clear whether effective management strategies can (will) be developed to deal with the specific problems associated with elasmobranch life-history patterns and the structure of elasmobranch fisheries. Factors such as bycatch, difficulty in obtaining accurate landing statistics due to the diffuse nature of the fish handling systems, low priorities assigned by management agencies due to low values of the landings, etc. make it difficult to develop and implement effective management measures.

How can fisheries scientists provide advice on the management of elasmobranch stocks given the above limitations? Intensive and extensive study of more than a few stocks does not appear to be a viable option. Therefore, we need to look at life-history patterns and processes in a more generic sense. Can we identify aspects of life history that appear to be strongly related to the ability of a species to withstand exploitation? Can we identify conditions that are useful indicators of overexploitation? If so, then we have a good chance of developing useful tools for planning and management.

Because of the importance of life-history pattern to fisheries management, it seems appropriate to begin this article with a consideration of just what "life-history pattern" means, how it is studied, and what it can tell us. We discuss the relevance of *r/K* selection theory to elasmobranch life-history studies and show how this paradigm provides guidance for estimating parameters needed for fisheries assessment and management.

Life-History Pattern and Strategy

Biologists frequently describe a species by a process akin to looking at a series of static 'snapshots" of the species in time. Description is based on a series of specimens of different sizes or ages. Such an account of the biology can be used to describe the "life-history pattern" of the species which, in the view of Horn (1978), implies the organism's lifetime pattern of growth, differentiation, storage, and especially reproduction. In our view, a more enlightening definition involves looking at the organisms in terms of their responses to environmental conditions. The life-history pattern of a species or a stock can be defined as the characteristic set of biological episodes and responses occurring during the lifetimes of the individuals in the population. These responses or episodes include where and when the animals are born, how long they remain there, how fast they grow, what and how much they eat, their social and sexual relationships, when and where and how often they mate, how many young are produced, their movements and migrations, and so on. Such definitions emphasize descriptive aspects of the morphology, physiology, and ecology of the species. The latter definition makes clear the plastic nature of life-history pattern by emphasizing the connection between environmental conditions and biological response. Inasmuch as environmental conditions vary from location to location and from year to year, the definition provides for variability in life-history traits both among individuals and among stocks within a species. And, inasmuch as environmental conditions vary over geological time, the latter definition also provides a link between life-history pattern and evolutionary trends.

Given a description of the life-history pattern of a species or a population, it is natural to ask why the animals have these particular traits or how this collection of traits arose. This leads to the idea of life-history strategy which Stearns (1976) describes as a research concept that combines the study of reproduction, growth, and genetics in an ecological setting to produce hypotheses concerning evolutionary changes. Here "strategy" is thought of as a set of traits brought about by natural selection to solve particular ecological problems. Simply put: in the game of life, an animal stakes its offspring against a capricious and unreliable environment. The animal wins the game if its offspring live to play another round. The appropriate tactics (pattern) for winning the game comprise the successful life-history strategy.

Life Histories in the Elasmobranchs

Any characteristic which affects the survival and reproduction of an animal is, by definition, a part of the life-history pattern of the species. This means there are an unlimited number of variables to observe and measure. Since this is obviously impossible, life-history studies necessarily concentrate on those aspects of the life history that seem most relevant to the research question of interest. Observations are generally made on composite variables or integrated responses, that is, on aspects of the life history which are, in themselves, the results of many other responses to environmental conditions. Some of the most reported aspects of life history are described below as they apply to the elasmobranchs.

Maximum Size—This is perhaps the most obvious character to study because it is easy to measure and tends

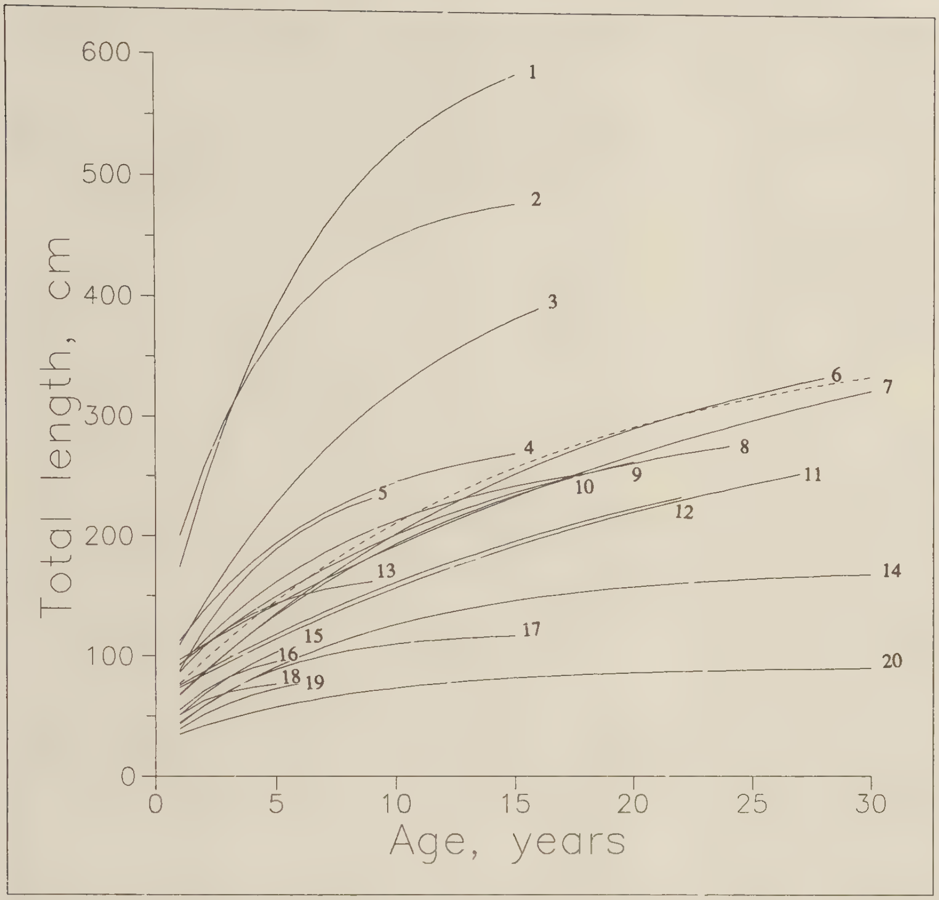

Figure 1.
Growth rates of sharks (solid lines) and of bluefin tuna (dashed line) (based on Hoenig 1979 and Brown 1988). Longevities shown are approximate, except that growth curves for *Squalus acanthias* and *Galeorhinus australis* are truncated at 30 years. Key to sharks: 1) *Alopias vulpinus* (female); 2) *Alopias vulpinus* (male); 3) *Galeorcerdo cuvieri*; 4) *Carcharhinus falciformis*; 5) *Prionace glauca*; 6) *Negraprion brevirostris*; 7) *Carcharhinus obscurus*; 8) *Isurus oxyrhinchus*; 9) *Sphyrna lewini*; 10) *Lamna nasus*; 11) *Carcharhinus leucus*; 12) *Carcharhinus plumbeus*; 13) *Carcharhinus limbatus*; 14) *Galeorhinus australis*; 15) *Mustelus californicus*; 16) *Rhizoprionodon terraenovae*; 17) *Galeorhinus japonicus*; 18) *Mustelus manzao*; 19) *Mustelus henlei*; 20) *Squalus acanthias*.

to be strongly related to a number of important processes such as consumption, mortality rate, and intrinsic rate of population increase (Blueweiss et al. 1978). The largest shark is the whale shark, *Rhincodon typus*, which reaches perhaps 2000 cm in length; the smallest squaloids and proscyllids reach maximum sizes a little above 20 cm. The largest shark is thus some two orders of magnitude longer than the smallest. This large range of sizes suggests that there should be interesting variability in other life-history parameters and processes within the elasmobranchs.

Most commercially utilized sharks are near the small end of the spectrum, measuring roughly a meter or two at full size (e.g., *Squalus acanthias*, *Mustelus* spp., *Galeorhinus* spp., *Scyliorhinus* spp.). However, the large sharks are actively sought by sport fishermen and are captured as bycatch in longline and other fisheries. Most of the commercially utilized skates and rays are under a meter in size (disc width).

Sexual Dimorphism in Size—Among the carcharhinid sharks, it is commonly observed that females grow to a larger size than males (Bigelow and Schroeder 1948). In other groups, sexual dimorphism in size may be absent or not very pronounced.

Individual Rates of Growth—Growth, the increase in somatic tissue over time, gives rise to the organism's final size and is obviously a major determinant of potential yield. Traditionally, elasmobranchs have been considered slow growing animals but this view has been subject to some misunderstanding. As in most other fishes, the rate of growth of a shark (in cm/yr) decreases continually as the shark ages (Fig. 1). Thus, a single parameter is insufficient to describe the growth rate of a species. Porbeagles, *Lamna nasus*, grow faster than dusky sharks, *Carcharhinus obscurus*, at early ages but by age 17 both species are the same size (roughly 250 cm total length). At ages greater than about 10 years, the annual growth of dusky sharks is greater than that of porbeagles. Which species "grows faster" is not readily apparent. In terms of total increase in length or weight per unit of time, a shark at almost any age will increase in size faster than a stickleback (*Gasterosteus* spp.), because sticklebacks attain such a small size. Perhaps more to the point, the growth curve for bluefin tuna, *Thunnus thynnus*, an extremely important commercial species, does not suggest faster growth than is found in a number of sharks (Fig. 1).

It is certainly true that the rate at which shark growth slows down with age tends to be very slow. The usual descriptor of fish growth is the familiar von Bertalanffy growth function

$$L_t = L_\infty(1 - e^{-k(t-t_0)}), \qquad (1)$$

where L_t is the length at age t, L_∞ is the asymptotic or ultimate length, k is the growth coefficient determining the degree of curvature or rate at which growth slows, and t_0 is a location parameter. Sharks tend to have among the lowest values of k of any fishes.

Finally, if we consider the amount of growth occurring in a shark population, averaged over the individuals in the population, then growth may be considered quite slow. This is because sharks tend to have low natural mortality and high longevity so that there are many old, slow growing individuals in the population. Thus, the production in a shark population tends to be low.

Energetics—Energetics refers to the amount of energy obtained from food by an animal, the efficiency with which this energy is assimilated, and the allocation of the energy to maintenance, growth, reproduction, and other life processes. Energetic relationships are dynamic and depend on the age or size of the animal, the environmental conditions (temperature, etc.) and the quality and quantity of the available food. Some elasmobranchs are sluggish; some capture prey by active pursuit or by ambushing passing animals. Many sharks are extremely active and some have even evolved the ability to maintain elevated body temperatures and to regulate body temperature to varying degrees (Carey et al. 1971). In general, little is known about energetic requirements and relationships in the elasmobranchs (Gruber 1984; Medved et al. 1988; Wetherbee et al. 1990) In their review of shark energetics, Wetherbee et al. found the following:

- food appears to pass through the alimentary tract of sharks more slowly than in teleosts; from the literature, estimates of the time required for a meal to be completely removed from the stomach range from 24 to 124 hours for five species of shark.
- the lemon shark, *N. brevirostris*, was observed to absorb energy from a meal with an efficiency comparable to that of most teleosts.
- estimates of daily ration for sharks are lower than for most teleosts; estimates for four species of shark range from 0.4 to 3.2% of body weight per day.

Only a few attempts have been made to estimate the annual consumption of prey by a shark population (Medved et al. 1988) and these estimates, in our opinion, are extremely rough.

Development—Development is the progressive differentiation of an organism. All of the elasmobranchs are born or hatched in a well-developed state. A few species of sharks, and many skates and rays, may attain sexual maturity within two years. But the majority of large sharks are slow to mature (Pratt and Casey 1990). Little is known about the control of onset of sexual maturity in sharks (Wourms et al. 1988). An important question is to what degree can development be speeded up by changing environmental conditions.

Reproduction—Tremendous variation is seen in the reproductive patterns in elasmobranchs including viviparity, oviparity and ovoviviparity, and even some unusual variations such as oviphagous (egg-eating) embryos. Detailed surveys of the modes of reproduction in the Chondrichthyes are presented by Wourms (1977), Wourms et al. (1988), and Otake (1990).

Despite the variation in observed pattern, a few features appear to be common to most, if not all, members of the group. All are iteroparous (reproducing more than once) rather than semelparous (producing all their young at one time). All produce young that are well-developed compared to the fragile early life stages of teleosts. All have severely limited numbers of young. Large blue sharks, *Prionace glauca*, and tiger sharks, *Galeocerdo cuvieri*, may produce more than 80 young at one time (Pratt 1979; Bigelow and Schroeder 1948), but most sharks produce far fewer. The bigeye thresher, *Alopias superciliosus*, produces two embryos at a time (Gruber and Compagno 1981). Female sharks produce young once or twice a year or every other year. Skates and rays also produce small numbers of young at a time but may continue to produce them throughout most of the year.

Parental Care—Sharks do not receive parental care as far as we know.

Mating Systems—There is no evidence that elasmobranchs have developed the wide variety of mating systems, such as long term pairing, polygyny, polyandry, and promiscuity, seen in birds and mammals. However, copulation has been observed in only a very few species (Clark 1963; Clark and von Schmidt 1965; Uchida 1990) and virtually nothing is known about social organization and possible mating systems. Tooth cuts on females in some species are perhaps indirect evidence of courtship activity (Stevens 1974; Pratt 1979).

Dispersal and Migration—Movements of sharks are an important aspect of life history inasmuch as they affect survival. We have much to learn about shark movements, but what we do know indicates that there is considerable variability among species. The movements of juvenile lemon sharks, *N. brevirostris*, appear to be extremely restricted (generally less than a mile) during the first several years of life (Gruber et al. 1988). Young sandbar sharks, *Carcharhinus plumbeus*, appear to be restricted to shallow areas during the warm part of the year but move to unknown locations in the winter (Springer 1960; Musick 1986). Tagging of adult sharks has shown that some species undertake spectacular long-distance movements including trans-Atlantic and trans-Pacific movements and movements between South America and the Canadian Atlantic (Olsen 1954; Holland 1957; Holden 1967; Stevens 1975; Templeman 1976; Casey et al. 1978). Only short-distance movements have been noted in other tagging studies. Interestingly, long-distance movements have been reported for some small species, notably the spiny dogfish, *S. acanthias*, and the school shark, *Galeorhinus australis*.

Social Segregation—It is commonly observed that catches of sharks have a preponderance of one sex or the other, or are composed of animals of a limited size range. Evidently, many species segregate by size and by sex (Pratt 1979). This type of segregation can be based on habitat, i.e., be local in nature, or occur on a wide geographical scale.

Storage of Energy—Sharks have large livers which store high-energy, fatty acids. Apparently, these lipids serve not only to provide buoyancy but also to provide stored resources for use during hard times (Oguri 1990). We believe a large liver is an adaptive character for predators that live under feast-or-famine regimes.

Longevity—Sharks are among the longest lived fishes. Based on vertebral rings or rings in dorsal spines, the following ages have been reported: for *S. acanthias*, 65–70 years (Ketchen 1975; Jones and Geen 1977); for the bull shark, *Carcharhinus leucus*, 27 years (Hoenig 1979); for the dusky shark, *C. obscurus*, 30 years (Hoenig 1979); for lemon sharks, *N. brevirostris*, 21 years (Brown and Gruber 1988). A school shark, *G. australis*, estimated to be at least 18 years old at the time of tagging was recaptured 25 years later, thus yielding an estimated age of 43 years (Anon. 1976). Grant et al. (1979) reported the recapture of six tagged school sharks that had remained at liberty from 23 years to 27 years and 8 months. The longevity of batoid fishes can also be high. Martin and Cailliett (1988) reported a maximum age of 23 years for female bat rays, *Myliobatis californica*, based on vertebral rings.

It is curious that the oldest ages reported for sharks are from two small species. High longevity is usually associated with large adult body size (Blueweiss et al. 1978). It should be noted that workers have had a great deal of difficulty procuring vertebral samples from large specimens, and methods for elucidating growth bands are still being developed; hence, the oldest ages may have been missed altogether.

Natural Mortality—Natural mortality differs from the other parameters considered so far in that it is a property of populations, not individuals. You cannot measure how fast an individual dies, because an individual can only be either alive or dead. Fishery scientists often estimate mortality rates from the age composition of a sample, but this is difficult for many shark species because the pattern of segregation by age makes it difficult to obtain an unbiased sample. Also, until the work of Stevens (1975), it was generally not considered possible to age sharks from vertebral rings. There are only a few direct estimates of natural mortality for sharks, notably: for the school shark, *G. australis*, 13% per year annual (finite) rate (Grant et al. 1979); for the porbeagle, *L. nasus*, 16% (Aasen 1963); for the spiny dogfish, *S. acanthias*, 9% (Wood et al. 1979). Natural mortality of adult little skate, *Raja erinacea*, was estimated to be 33% (Johnson 1979). The paucity of information on mortality led Hoenig (1983) to suggest using the relationship between longevity and mortality to estimate mortality rates.

Intrinsic Rate of Population Increase, *r*—This is another property of populations rather than of individuals. We defer a formal definition to the section on r/K selection theory and note here that this parameter describes the innate or intrinsic ability of a population to increase in size when confronted with favorable environmental conditions. For example, if the size of a population is reduced by temporary fishing, then crowding and competition for resources should be reduced. This should result in an opportunity for the population to grow back to its former size once fishing is reduced. The parameter r is a composite of many factors which determine population growth through three mechanisms:

- changes in individual body growth rates
- changes in natural mortality
- changes in reproduction.

Intrinsic rate of increase has been studied in the laboratory for a few species only, mostly micro-organisms and insects. Observations on population increase in the wild are even more scarce. However, one can calculate this quantity from some types of commercial fisheries data, such as from the parameters of a Schaefer (1957) stock production model. Life table, Leslie matrix, and other ''book keeping'' types of models can be used to estimate ''observed rate of increase'', which may be considered a minimal estimate of intrinsic rate of population increase.

No estimates of intrinsic rate of population increase are available for elasmobranchs. However, as we shall see, there are some indirect methods appropriate for estimating this quantity.

What Do Life-History Studies Tell Us?

Clearly, many of the parameters estimated in a study of life history, such as growth and mortality rates, have immediate management value as input to assessment models. Even when insufficient information has been collected to conduct a complete assessment of a stock, the available information may still provide valuable guidance. For example, if a comparative study shows two parameters such as natural mortality and longevity to be closely related (Tanaka 1960; Hoenig 1983; Hoenig et al. 1987), then the information on one parameter may be used to estimate the value of the other from a regression relationship. Even if the available information is inadequate to develop estimates of all parameters needed for assessment models, it may still be possible to make qualitative statements about the need for regulation based on the "assessment by analogy" concept (Hoenig et al. 1987). Thus, one might speculate that if conditions in a fishery of interest are similar to those observed in another fishery known to be over-exploited, then by analogy the fishery of interest may also be in need of regulation. Symptoms of overexploitation have been described for populations of teleosts by the Strategic Planning for Ontario Fisheries (SPOF) Working Group (1983) but a comparable list for elasmobranchs has yet to be developed. Such a list would probably rely heavily on changes in baseline (preferably pre-exploitation) life-history parameter values. Signs of overexploitation might include increase in growth rates and fecundity, reduction in mean age and mean size in the population, reduction in age at maturity, reduction in the proportion of females that are gravid or carrying sperm in the oviducal gland, etc.

Life-history studies can provide massive amounts of information with potential uses in a number of disciplines. The questions then become "How can we assimilate and synthesize this information?" and "Is there any logical framework for explaining the observed variability in life-history parameters?" From a practical point of view, such a framework is needed to suggest comparative studies that might result in useful methods for estimating parameters, to provide guidance in determining what parameters may be useful in identifying overexploitation, and for developing methods to rank species according to their resilience to exploitation. We believe that *r*/*K* selection theory is useful for these purposes.

r/*K* Selection Theory

The theory of *r*/*K* selection has been around for quite awhile (MacArthur and Wilson 1967) and it has its share of adherents and critics. It is intimately related to the logistic model of population growth (whose parameters are "*r*" and "*K*"), and the logistic model provides the theoretical basis for the stock production model of Schaefer (1957). It is thus of interest to study the connections between *r*/*K* selection theory and fisheries management models.

Let us begin with a consideration of the logistic model of population growth. Though the logistic curve dates back to Verhulst in the early nineteenth century, modern interest in the logistic model can be traced to Lotka's (1925) work on human populations and to Volterra's (1928) work on fish. Imagine an undisturbed population inhabiting a constant environment for a long period of time. The population has reached an equilibrium state so that the number of births exactly balances the number of deaths and the number of animals present remains constant (Fig. 2). Now suppose that some kind of catastrophic event occurs and the population is suddenly reduced. One would expect that there must be some way for the population to recover, otherwise every successive catastrophic event would push the population closer to extinction. With reduced numbers present, more resources become available for each individual so the survival rate might increase. With more energy available, the organisms should be able to devote more effort to growth and reproduction. Thus, we might see an s-shaped recovery curve for population size as a function of time. This is the logistic model which says, in essence, that in a salubrious and uncrowded environment, where there are no resource limitations, the population growth trajectory may approach an exponential curve, but as the population increases resources again become limiting and the population growth approaches zero. Mathematically, the rate of population increase, dN_t/dt, can be described by

$$dN_t/dt = r\,N_t\,(K - N_t)/K, \qquad (2)$$

where N_t is the population size (in numbers or in biomass) at time t, K is the maximum (asymptotic) size of the population and is usually called the carrying capacity of the environment, and r is a scale parameter which controls how fast the population can increase. The parameter r is known as the intrinsic rate of population increase. Equation (2) describes the rate of growth at any particular population size. To determine the size of the population at any time we need to integrate Equation (2). Thus, the population size at time t is given by the s-shaped curve (Fig. 2)

$$N_t = K/(1 + b\,e^{-rt}), \qquad (3)$$

where b is a location parameter which is related to the size of the population at time $t = 0$.

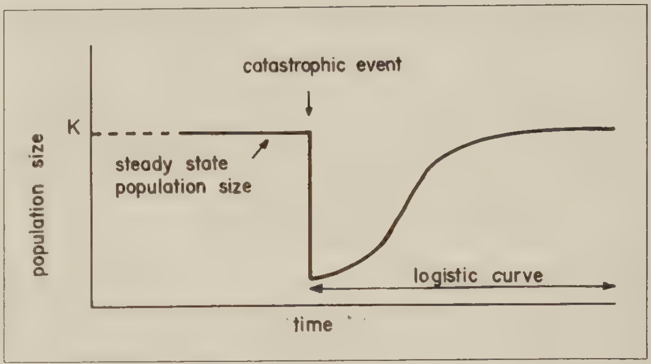

Figure 2.
Representation of population size of a hypothetical population over time. Population begins at equilibrium at the carrying capacity of the environment, undergoes a catastrophic decline, and recovers according to the logistic model of population growth. *K* is the maximum (asymptotic) size of the population.

Note that when N_t is close to zero, the factor $(K - N_t)/K$ in Equation (2) is close to 1. So, the rate of change of the population at low population sizes is close to

$$dN_t/dt \approx r\, N_t. \tag{4}$$

Expressed in words, the rate of growth is proportional to the size of the population present and the growth over time is similar to the growth of money in a savings bank. More formally, the integrated form of (4) is given by the exponential curve

$$N_t = N_0\, e^{rt}, \tag{5}$$

where N_0 is the initial size of the population (at $t = 0$).

Consider a species that lives in an unstable, unpredictable environment. Such a species suffers catastrophes often and must be biologically adapted to respond quickly to new, uncrowded conditions. Thus, it must have a high value of "r." In contrast, a species living in a very stable environment must be able to withstand competition and use its limited resources efficiently but need not necessarily be equipped to deal with sudden, dramatic shifts in environmental conditions. It must be adapted for conditions at or near the carrying capacity of the environment. We say that the former type of species is r-selected while the latter is K-selected.

The appeal of this concept is that it provides a framework for judging the evolutionary and survival values of life history traits. That is, we can predict that certain traits would tend to be found in r-selected species while others would be found in K-selected species. Ricklefs (1979) and others list the following characteristics:

r-selected traits	K-selected traits
chooses variable and/or unpredictable habitats	chooses constant and/or predictable habitats
frequently colonizes or recolonizes	rarely colonizes or recolonizes
niche broad	niche narrow
"small" body size	"large" body size
rapid development	slow development
high fecundity	low fecundity
early reproduction	delayed reproduction
semelparity	iteroparity
high and/or catastrophic mortality; density independent mortality	low and/or constant mortality; density dependent mortality
short longevity	long longevity
highly productive	highly efficient at producing biomass

To the list of K-selected traits can be added elaborate social structures and mating systems, parental care of young, and storage of energy.

Based on the description in the last section of common life-history features of sharks, it would appear that this group is extremely K-selected. If the r/K selection theory holds up under scrutiny, then it is of interest to ask to what extent can the theory be refined. The following question arises: Can we rank species along an r-K continuum and would this ranking provide some indication of the relative abilities of the species to withstand exploitation?

The theory of r/K selection has received wide attention and there are a number of generalizations, including a stochastic version of the theory known as bet hedging and the formulation of another type of selection called α-selection (see Emlen 1973). The latter concept deals with the depression in the rate of population increase due to interaction with other species. A species is called α-selected if it has evolved mechanisms to avoid competitive inhibition.

There are also a number of criticisms of the overall theory. One criticism, that the r/K selection theory doesn't answer all questions, can be dismissed out of hand since, for our purposes, we only need a theory that will provide useful information or predictions for management. That this criticism has been raised at all may be attributed to the high hopes that were generated by the formulation of r/K selection theory.

A more serious criticism is that the theory doesn't always seem to apply. For example, sticklebacks (*Gasterosteus* spp.) have small body sizes, short life spans, and other characteristics normally associated with r-selection but also have low fecundity and parental care of the young which is associated with K-selection. Stearns (1977) analyzed 35 studies and found that 17 species did not fit the r/K selection scheme. Still, that a simple and rather intuitive theory worked in about half the cases argues that it is still worth considering.

Another criticism is that the theory hasn't been tested properly. It is easy to list traits that one imagines should be associated with r- or K-selection and then to list species which fall near one extreme or the other. Ricklefs (1979) argues that one should also determine whether the species presumed to be r-selected face greater environmental variability and have greater variability in numbers than those presumed to be K-selected.

Four counter-arguments can be made to the last criticism. First, might not the consistent co-occurrence of traits associated with each extreme be viewed as supportive of the theory? Ricklefs (1979) argues that many life-history traits are correlated with body size and that biophysical differences in scale, rather than evolutionary selection, may account for small animals having "r-selected" traits relative to larger animals. This argument of scale would not apply within a narrow size range. Second, in some cases it can be proved mathematically that a trait will be selected for (or against) in an unstable environment. Third, Emlen (1973) argues that "Populations held by inclement weather or predation to levels well below their carrying capacities experience primarily r_0-selection [i.e., r-selection]..." Thus, according to this view, great variability in environment or population size is not necessary to validate the model. However, we run into a difficulty with the definition of carrying capacity. Consider a hypothetical, stable population which experiences some predation as part of its normal course of events. Is this population at the carrying capacity of its environment or is it held at a lower level by predators? In other words, is the carrying capacity a natural level of population size or is it a concept that only applies to an animal completely divorced from its natural environment? We leave it to others to grapple with this question. The interested reader should consider studies by Pauly (1979) and Larkin and Gazey (1982). The fourth counter-argument to the criticism of lack of validation is that one can estimate the intrinsic rate of increase in some cases and thus we can see how *r*-selected are the species that we have presumed to be in this category.

Estimating the Rate of Population Increase

Estimating the Value of *r* from a Logistic Stock Production Model

The rate of growth of a population depends on the size of the population relative to the carrying capacity, as described by Equation (2). This curve is a dome-shaped, parabolic function of population size. Now, suppose the population is harvested at exactly the same rate at which the population is growing, i.e., at the rate dN/dt. Then harvest will just equal production and the population will maintain a steady state at the population size N. This level of harvest is known as "surplus production" because it can be continuously removed without lowering the population size. Thus, the sustainable yield is a parabolic function of population size. If one could observe the steady yields obtained at two or more points of time when the population size is also known, then one could solve for (estimate) the parameters r and K. This is the basis of Graham's (1935) production model.

It is important to recognize that catch is not necessarily synonymous with production—they are synonymous only under equilibrium conditions. Thus, if 500 tons of biomass (say) are suddenly removed from an unexploited population, the population production will rise in response to the removal. But, the removal itself is not surplus production. If one treats all biomass removal as if it were removal of surplus production, one will tend to overestimate the value of the maximum sustainable yield. In a developing shark fishery, much of the harvesting may amount to simple biomass removal rather than removal of surplus production. This is particularly true if the fishery develops rapidly. Reduction of the population cannot continue indefinitely, or one will observe a "boom or bust" type fishery. This does not mean that a sustained harvest cannot be maintained at a sufficiently low level.

Although it is at least conceptually easy to measure the catch from a fishery, it is difficult to estimate population size. However, it is well known that sustainable yield under a logistic model is also given by

$$Y = K F - (K/r) F^2, \qquad (6)$$

where F is the instantaneous rate of fishing mortality (see Ricker 1975, p. 315). Furthermore, fishing mortality is generally assumed to be proportional to fishing effort, i.e.,

$$q f = F, \qquad (7)$$

where f is the fishing effort and q is known as the catchability coefficient. Therefore, sustainable yield is also a parabolic function of fishing effort (Schaefer 1957):

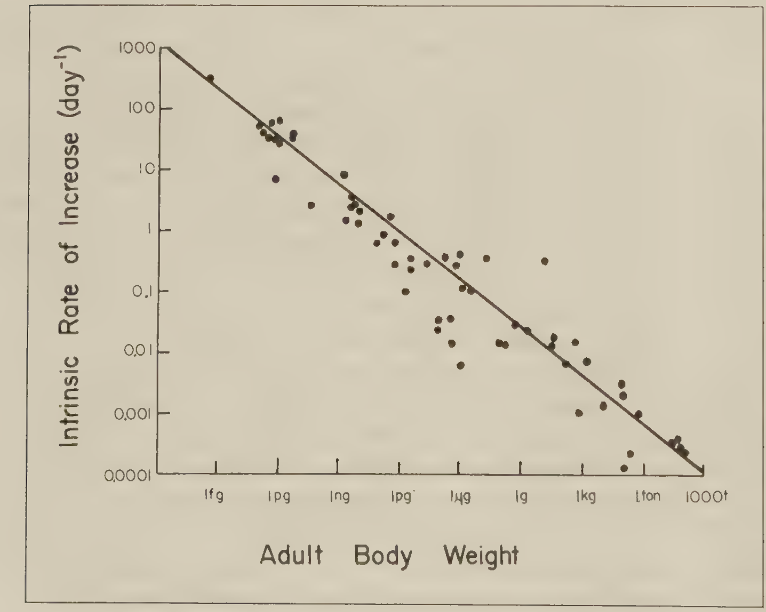

Figure 3.
Relationship between the estimated intrinsic rate of increase of various organisms and their adult body weight (modified from Blueweiss et al. 1978 by Pauly 1982).

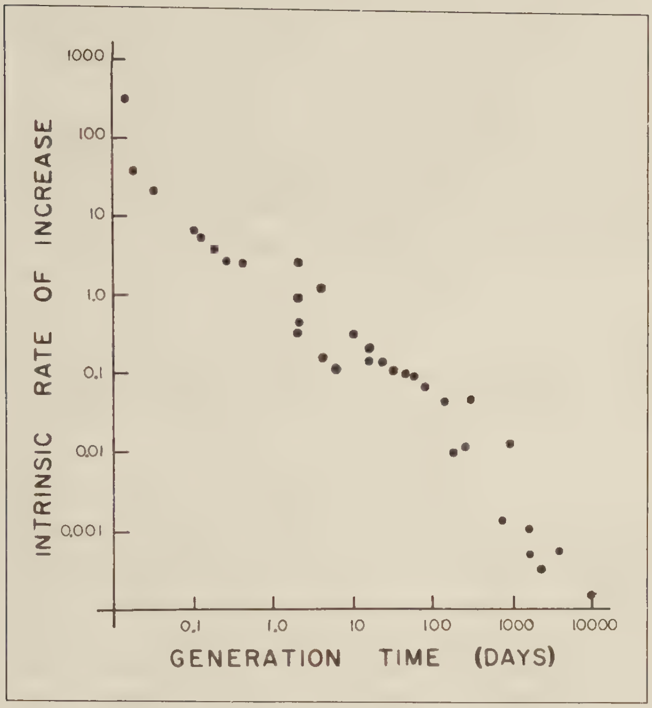

Figure 4.
Relationship between the estimated intrinsic rate of increase of various organisms and the generation time (modified from Heron 1972).

$$Y = (K q) f - (K q^2/r) f^2. \tag{8}$$

The stock production model can be fitted to observations on catches and the corresponding fishing mortalities (when conditions in the fishery are at equilibrium, i.e., stable) in order to obtain estimates of maximum sustainable yield, optimum fishing mortality, etc., as well as estimates of r and K. The model can also be fitted to observations on catch and effort (or catch rate and effort), but some additional information is needed to estimate q in order to obtain estimates of r and K.

Stock production data are notoriously variable and it is difficult to meet the equilibrium assumption of the model. A number of methods have been developed to deal with these problems (see, e.g., Gulland 1983; Schnute 1977). But, it is not clear whether a comparative study of estimates of r from production models would lead to useful generalizations though this was suggested by Caddy and Csirke (1983).

Comparative Studies of *r*

A number of estimates of intrinsic rate of increase, r, are available in the literature for organisms ranging in size from viruses to whales (24 orders of magnitude). Most estimates are based on laboratory studies. The intrinsic rate of increase appears strongly related to adult body size and to generation time (Figs. 3, 4). It is not clear how useful these relationships would be over a small portion of the range of the explanatory variable (body weight or generation time) though the relationship in Figure 5, dealing with fishes and whales, is encouraging. Indeed, Pauly (1982) suggested that the intrinsic rate of increase (per day) might be estimated, albeit crudely, from the regression model

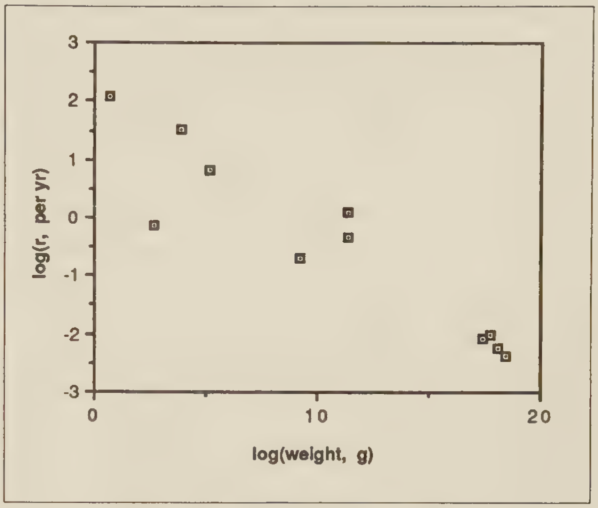

Figure 5.
Relationship between estimated intrinsic rate of increase of fishes and whales and their adult body weight. (Data from Pauly [1982] plus an additional case [courtesy of Alec MacCall, National Marine Fisheries Service, Tiburon, CA, personal communication, summer, 1983]: northern anchovy (*Engraulis mordax*) off California, $r = 0.88\ \text{yr}^{-1}$, $w = 15$ g.)

$$r = 0.025\, w^{-0.26}, \tag{9}$$

where w is defined to be the mean of the weight at first maturity and the maximum weight (both expressed in grams). Based on this, the maximum sustainable yield can be estimated as (Ricker 1975, p. 315)

$$\text{MSY} = r K/4. \tag{10}$$

"Book Keeping" Methods for Estimating Rate of Population Growth

It is also possible to estimate the observed (rather than the intrinsic) rate of population increase from schedules of age-specific survival and fertility. Either a life table or Leslie matrix model approach can be used. These methods essentially project a population forward in time and keep track of all survivors and offspring. We will consider the use of the Leslie model as described by Vaughan and Saila (1976).

Suppose we have data of the following sort:

Age, i	Survival, S_i	Female offspring, b_i
0	0.50	0
1	0.85	0
2	0.85	0
.	.	.
.	.	.
.	.	.
11	0.85	0
12	0.85	2.5
13	0.85	2.5
.	.	.
.	.	.
.	.	.
24	0.85	2.5
25	0	2.5

These data are based on the life history of the lemon shark, *N. brevirostris*. Based on tetracycline validated growth marks in vertebral centra, Brown (1988) reported the age at maturity for females to be approximately 13 years and the oldest age observed to be 21 years. Longevity is probably somewhat higher since the largest specimens examined were considerably smaller than the maximum reported size. A longevity of 26 years suggests, on the basis of a regression relating mortality to longevity (Hoenig 1983), that the annual survival rate is around 85%. Alternatively, an estimate of instantaneous natural mortality, M, can be obtained from Pauly's (1980) regression relating mortality to von Bertalanffy growth parameters and mean water temperature. Assuming a mean water temperature of 24°C (Gruber, unpubl. observations) and the von Bertalanffy parameter estimates in Brown (1988), one arrives at an estimate of M of 0.12 which corresponds to an annual survival of 89%. Litter size is around 8 to 12, of which half are females (Clark and von Schmidt 1965). Females in the related species (*Negaprion acutidens*) bear litters every other year (Stevens 1984) as apparently do females of *N. brevirostris*. Hence each female produces 2.5 females per year on average. Survival rate in the first year is estimated to be 50% (Gruber, unpubl. research).

Suppose further that the age composition in a certain year t is the following:

Age	Number at age
0	n_{0t}
1	n_{1t}
2	n_{2t}
.	.
.	.
.	.
25	n_{25t}

Then we can calculate the age composition in the next year, i.e., at time $t + 1$. The number of newborns will be the sum of the offspring produced by each age in year t:

$$n_{0,t+1} = \sum_{i=0}^{25} n_{it}\, b_i$$

$$= n_{0t} \cdot 0 + n_{1t} \cdot 0 + \ldots + n_{25t} \cdot 2.5. \quad (11)$$

The number of one-year olds will be equal to the number of age–0 animals which survive to the next year:

$$n_{1,t+1} = n_{0t} \cdot s_0 = n_{0t} \cdot 0.5.$$

Similarly, the number at any age i (above age 0) in year $t + 1$ is given by

$$n_{i,t+1} = n_{i-1,t} \cdot s_{i-1}. \quad (12)$$

These relationships can be expressed compactly in matrix notation. Define the population projection matrix A to be

$$A = \begin{bmatrix} b_0 & b_1 & b_2 & \cdots & & b_{25} \\ s_0 & & & & & \\ & s_1 & & & 0 & \\ & & s_2 & & & \\ & & & \ddots & & \\ & 0 & & & \cdot & \\ & & & & s_{24} & \end{bmatrix}. \quad (13)$$

(All elements of A are zero except the first row and the first subdiagonal.) Also, denote the population age structure at time t by

$$N_t = \begin{bmatrix} n_{0t} \\ n_{1t} \\ n_{2t} \\ \cdot \\ \cdot \\ \cdot \\ n_{25t} \end{bmatrix}. \quad (14)$$

Then the population at time $t + 1$ can be found by

$$N_{t+1} = A\, N_t. \quad (15)$$

The rate of population increase, $r(\text{obs})$, can be found from the largest eigenvalue (λ) of the matrix A by the relationship $r(\text{obs}) = \log_e(\lambda)$ (Vaughan and Saila 1976). However, Vaughan (1977) provided a more direct method for finding the rate of increase as the solution of the following equation:

$$\frac{e^{r(\text{obs})}}{s_0} = b_1 + \sum_{i=0}^{I} b_{i+1} e^{-i\, r(\text{obs})} \prod_{j=0}^{i} s_j, \quad (16)$$

where I is the oldest age class in the population (starting with age 0).

Since it may be difficult to interpret a value of $r(\text{obs})$, a convenient alternative is to compute the theoretical doubling time for the population. Under exponential growth, the population size at time t is

$$N_t = N_0 \, e^{r(\text{obs})t}$$

so

$$\frac{N_t}{N_0} = e^{r(obs)t}.$$

Setting N_t/N_0 equal to 2 and solving for t gives

$$\text{time to double} = \frac{\log_e 2}{r(\text{obs})}. \tag{17}$$

This computed time-to-double will equal the actual doubling time if the population has a stable age distribution; otherwise, the computed doubling time may be larger or smaller than the actual doubling time. Nonetheless, Equation (17) provides a useful way to visualize the significance of a value of $r(\text{obs})$. Another possibility would be to compute the annual percentage change in population size under the same assumption of a stable age distribution.

Estimating age-specific fertility is generally feasible. Estimating survival rates is more difficult but can still be done. However, among teleosts, the first year survival rate is so highly variable and so difficult to measure, that estimates are of questionable use.

The elasmobranchs present a very different situation. The small numbers of well-developed young suggest that first year survival is stable and fairly similar to juvenile and adult survival. As a consequence of the elasmobranch life-history pattern, the Leslie model may prove useful for management of these fishes in three ways.

First, if all survival rates (including first year) are known, then the rate of population increase can be calculated using Equation (16) (Vaughan 1977). (Note that the rate of increase obtained in this way refers to growth in numbers rather than to growth in biomass.) Second, if all survival rates except that in the first year are known, and if the population is assumed to be at equilibrium, then first year survival can be calculated from Equation (16). One can thus study the effects of changes in parameters on the rate of increase and the first year survival rate. For example, one could calculate what would be the rate of increase if all young survived their first year of life or if first year survival equalled that of adults. In this way, one can explore the probable upper limits to the intrinsic rate of increase. Third, the Leslie matrix can be used to model the time to recovery of a depressed population. Schaaf et al. (1987) compared, for various species of teleosts, the time it takes to recover (to 80% of the initial abundance) following a one-time catastrophic reduction in survival of young-of-the-year fish, e.g., as the consequence of a pollution incident. They assumed no compensatory mechanisms were operative. For elasmobranchs, studies can be directed towards determining the length of time to recovery for various species following cessation of fishing under a variety of scenarios of compensation. For example, one might assume that first year survival increases to the adult level, age of maturity is reduced by one or two years, fertility increases 25%, etc.

Consider the lemon shark data in the text table. The computed value of $r(\text{obs})$, based on these parameter values, is 0.015 yr^{-1}, corresponding to a doubling time of 46 yr (Table 1). Since lemon sharks are not believed to have been heavily exploited at the time these estimates of life-history parameters were made, the parameter estimates ought to imply a rate of increase close to zero (i.e., a large doubling time or, if the estimate is negative, a large halving time). This prediction is borne out by the assumed parameter values but this result may be fortuitous. A first-order sensitivity analysis suggests that $r(\text{obs})$ may be in the range -0.04 to 0.07 with a corresponding wide range of doubling times (lines 2 through 10, Table 1) . Thus, it appears that apparently minor changes in parameter values can have significant effects on population dynamics. The results also suggest that it may be difficult to estimate life-history parameters with sufficient precision to understand the dynamics of a specific population.

If the lemon shark population is assumed to be at equilibrium ($r(\text{obs}) = 0.0$), then the first year survival rate would have to be 39% to balance Equation (16), given the parameter values in line 1 of Table 2. First-year survival rate computed under a variety of seemingly plausible scenarios ranges from 16 to 97% (Table 2). For example, if survival of all age groups (except the young of the year) decreases from 85% to 80%, then first year survival would have to rise to 96% to prevent a decline in population, all other things being constant.

Applications to Fisheries Management

The foregoing provides a number of ways in which the consideration of life-history patterns and r/K selection theory can provide guidance in the management of elasmobranch stocks. First, certain life-history parameters (natural mortality, growth, etc.) enter directly into fisheries assessment models. Estimation of population parameters is an inexact science, so it is important to assess the possibility of errors in the information available for assessment. A reasonable approach is to compare parameter estimates for one species with those for a similar species. This idea is easily generalized to enable one to consider patterns in parameter values among species. Indeed, some parameters appear to be so closely correlated that information on one easily estimated parameter can be used to estimate another, more difficult

Table 1.

Computation of population rate of increase, r (obs), and doubling time, $t(d)$, of lemon sharks (*N. brevirostris*) from a Leslie matrix model. The first line represents baseline conditions, i.e., computations based on best available information.

Assumed parameter values[a]					Computed results[b]			
t(mat)	t(max)	b	S	S_0	r (obs)	% change	$t(d)$	% change
12	26	2.5	0.85	0.50	0.015	—	46	—
11	26	2.5	0.85	0.50	0.028	84	25	− 46
13	26	2.5	0.85	0.50	0.004	− 76	191	312
12	25	2.5	0.85	0.50	0.014	− 6	49	7
12	27	2.5	0.85	0.50	0.016	5	44	− 5
12	26	2.0	0.85	0.50	0.001	− 93	624	1246
12	26	3.0	0.85	0.50	0.026	76	26	− 43
12	26	2.5	0.80	0.50	− 0.042	− 380	− 17	− 136
12	26	2.5	0.90	0.50	0.068	358	10	− 78
12	26	2.5	0.85	0.45	0.008	− 44	83	78
12	26	2.5	0.85	0.55	0.021	40	33	− 28

[a] t(mat) = age of maturity; t(max) = maximum (truncated) age; b = number of females born per mature female per year; S = annual survival rate after the first year of life; S_0 = probability of surviving the first year of life.

[b] r(obs) = observed or realized rate of population increase per year; $t(d)$ = theoretical doubling time in years corresponding to r (obs), assuming a stable age distribution. % change is the percentage change relative to base-line conditions.

Table 2.

Computation of first-year survival rate, S_0, of lemon sharks (*N. brevirostris*) from a Leslie matrix model. The first line represents base-line conditions, i.e., computations based on best available information. Symbols are as defined in Table 1.

Assumed parameter values					Computed results	
t(mat)	t(max)	b	S	r (obs)	S_0	% change
12	26	2.5	0.85	0	0.39	—
11	26	2.5	0.85	0	0.33	− 16
13	26	2.5	0.85	0	0.47	20
12	25	2.5	0.85	0	0.40	2
12	27	2.5	0.85	0	0.39	− 1
12	26	2.0	0.85	0	0.49	25
12	26	3.0	0.85	0	0.33	− 17
12	26	2.5	0.80	0	0.97	146
12	26	2.5	0.90	0	0.16	− 59

to estimate parameter. We have already considered the estimation of intrinsic rate of increase from adult weight and generation time (Figs. 3–5). Another example is the estimation of natural mortality rate from longevity (Fig. 6) or from von Bertalanffy growth parameters and water temperature (Pauly 1980). This approach is becoming increasingly popular (Adams 1980; Gunderson 1980; Myers and Doyle 1983; Gunderson and Dygert 1988). These comparative approaches are admittedly crude but they are surely better than nothing.

Because many elasmobranchs currently have a relatively low commercial value or are harvested by difficult to sample sport fisheries, it seems likely that assessment models and regulations will have to be based on incomplete information. For this reason, we have explored a number of simple approaches for assessing stocks, such as monitoring changes in growth rates and other life-history parameters. This obviously requires good baseline data. We have hinted that it may be possible to develop criteria for ranking species according to their capacity to withstand exploitation. From r/K selection theory, we are led to believe that natural mortality rate, age at maturity, and fecundity may be useful for these purposes. The intrinsic rate of increase should be a most useful criterion for ranking species but this parameter is difficult to measure. Fortunately, intrinsic rate of increase and natural mortality appear to be closely related to other parameters such as growth and longevity so that there may be simple ways to obtain approximate values.

Monitoring stock abundance could provide useful management information for those species that can be effectively sampled. These might include species that have well defined nursery areas in bays and lagoons. However, many species have complicated, poorly understood distributional patterns which vary with sex, size, and season. Designing effective, fishery-independent sampling programs is likely to be exceedingly difficult for these species.

The Leslie matrix model (or similar age-structured model) appears to be a useful way to simulate elasmobranch populations. In the absence of sufficient fisheries data, biologists will probably have to settle for experiments with these simulated populations in order to develop management strategies. We have already shown how the Leslie model can be used to estimate survival in the first year of life and to place bounds on the probable value of the

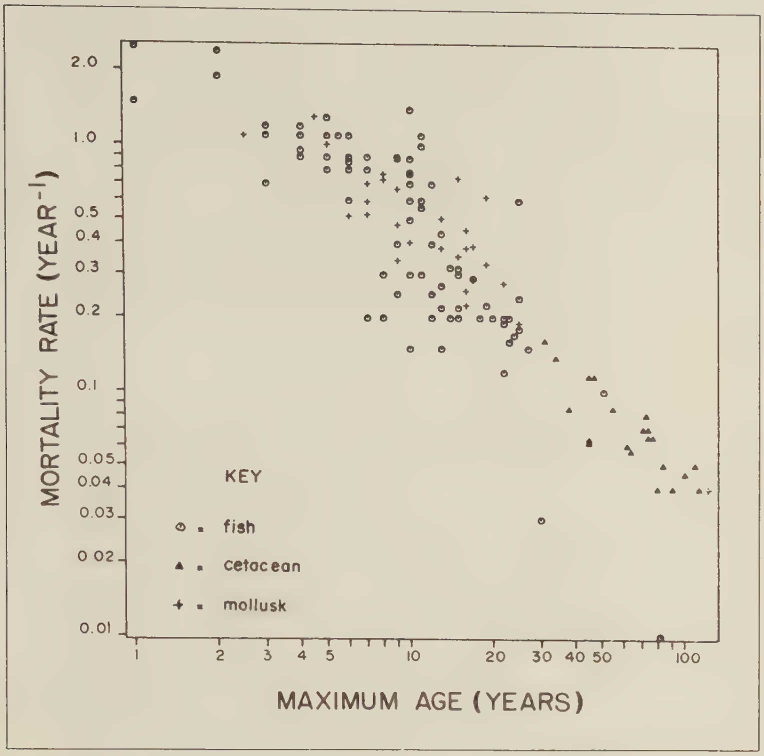

Figure 6.
Relationship between the estimated instantaneous mortality rate and the maximum age known for 125 stocks of fish, mollusks, and cetaceans (from Hoenig 1983).

intrinsic rate of increase. It might also be used to determine how much fecundity/first year survival must change in order to compensate for an increase in adult mortality. Grant et al. (1979) suggested as a rule of thumb that harvest should be controlled so that the production of young did not fall below 50% of the unexploited level. They did not explore the consequences of this assumption in terms of required changes in life-history parameters. The model can also be used to study recovery times following a decrease in fishing mortality.

A number of workers have suggested that egg-per-recruit analysis is a useful tool for fishery management (e.g., Prager et al. 1987). This concept pertains to equilibrium situations and is difficult to interpret unless the egg-per-recruit is compared to the virgin (unexploited) level. Computation of egg production as a percentage of the virgin level is straight forward and can be applied to both equilibrium and nonequilibrium situations. It remains to be seen how well the 50% rule of Grant et al. (1979) works in practice.

The Leslie matrix model would be useful for evaluating the consequences of harvesting "surplus" males while protecting females. Many terrestrial big game populations are managed in this manner. Since the males of all elasmobranchs are readily identified by the presence of external claspers and many elasmobranchs segregate by size and sex, this approach may be feasible for many species, particularly for large sharks. The evaluation of such a management scheme should be based on monitoring the abundance of juveniles or the frequency of occurrence of gravid females over time and, for those species which store sperm, the proportion of females retaining sperm in the oviducal gland. In theory, a differential harvest of the sexes could provide a sound basis for the application of change in ratio techniques for estimating population size and other parameters (Seber 1982). This would require accurate catch statistics and accurate fishery-independent assessments of sex ratios and thus does not appear to be a viable option for widespread use.

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Early Life-History Implications of Selected Carcharhinoid and Lamnoid Sharks of the Northwest Atlantic

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ABSTRACT

The size of most newborn sharks makes them susceptible to predation from their own kind and other large fishes. In the northwestern Atlantic, juvenile nursery grounds can be generally classified according to whether or not the young are exposed to such predatory risk. Several related factors—breeding frequency, litter size, size at birth, early growth rate—may help offset early natural mortality. These factors are counterbalanced by the different species in several different ways, producing numerous early life history strategies. In general, slow growing species are either born at relatively large sizes or use protected nursery grounds, whereas faster growing species tend to rely more on growth rates than the other factors.

Introduction

An expanding U.S. recreational (Casey and Hoey 1985) and commercial (Anderson 1985) fishery for sharks in the northwestern Atlantic may be exceeding the estimated maximum sustainable yield (National Oceanic and Atmospheric Administration 1978; Gulf of Mexico Fishery Management Council 1980). Additionally, a long established fishery in Cuba (Anderson 1985) and a strong and growing shark fishery in Mexico (Bonfil et al. 1990) targets the same stock. Management of this stock may soon be necessary which will require detailed life-history information for estimations of stock potential.

Because of the data needed in life-history studies, research often focuses on the adult portions of the stock for information (i.e., reproduction and maturation). Hoenig and Gruber (1990) point out that a successful life-history strategy is one where the offspring survive to play another round in the "game of life"; unfortunately, little attention is sometimes paid to the early life-history of most species, although this may be a critical period for certain characteristics—recruitment, survival, and mortality (Hoff and Musick 1990).

For sharks, a successful strategy has been attained by the counterbalancing of several interrelated factors—reproductive frequency, size at birth, litter size, growth rate, and the use of nursery areas (Fig. 1). Viviparous sharks, in general, are *K* strategists (Pianka 1971; Holden 1977). They are relatively long-lived and slow growing with reproductive energy expended in the production of a relatively small number of precocious young after a lengthy gestation period (see Cailliet et al. 1986; Cailliet 1990 for a review). Viviparity restricts fecundity, thus there is a direct relationship between the number and/or size of the young produced and the size of the mother. For several carcharhinid species, the smaller (younger) the mother, the fewer the number of offspring produced per litter (Bass et al. 1973; Parsons 1983b; S. Branstetter, unpubl. data). Additionally, the inverse relationship between number and size of embryos per litter documented for the Atlantic sharpnose shark, *Rhizoprionodon terraenovae* (Parsons 1983b), should be expected for most viviparous species. Given the limited space available to carry young, a female can produce either a large number of small young, or a small number of large young.

Shark pups are precocious, and cohort survival may be dependent on an early life history that allows for attainment of a certain minimum size which both deters predators and increases swimming efficiency and speed (Thompson and Simanek 1977; Webb and Keyes 1982) so that the individual can actively avoid predation. It is unlikely that food is a major limiting factor to their survival, considering that the young usually occupy estuarine or coastal habitats that are also occupied by numerous fish and invertebrate species which serve as available prey items for these opportunistic feeders. Young sandbar sharks are able to selectively feed on specific prey items (Medved and Marshall 1981; Medved et al. 1985, 1988). Additionally, based on the high oil content in the livers of immature sharks, Springer (1967) postulated that they have little difficulty finding sufficient food. Thus predation may be the most important source of mortality on the young sharks.

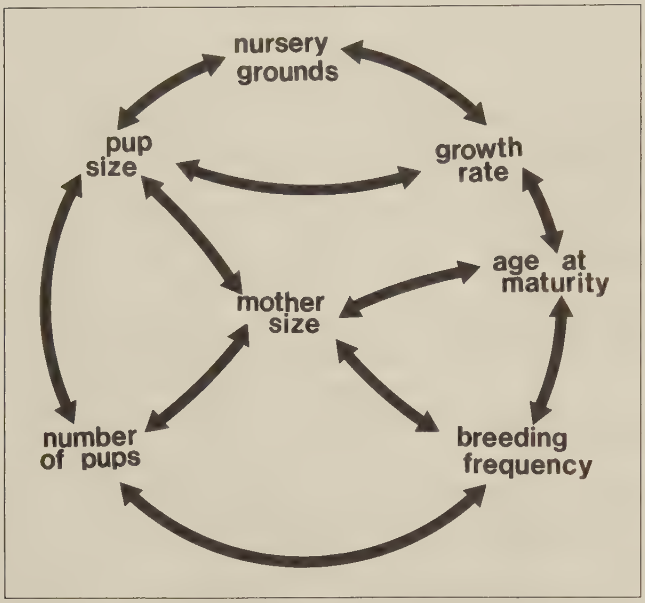

Figure 1.
Generalized interrelationship of life-history characteristics for viviparous shark species.

Predatory risk to the young may be greatest from other sharks, especially adult sharks, and other large fishes such as grouper (Randall 1977) may also be a source of natural mortality. Small sharks, either young sharks or adults of small species, are frequently recorded as food items of larger sharks (Castro 1983). Usually, greater than 50% of shark stomachs are empty upon examination, even when collected by passive (nonattracting) methods such as gill nets (Bass et al. 1973; Snelson et al. 1984; Killam 1987). Few detailed quantitative food habits studies exist (Medved and Marshall 1981; Stillwell and Kohler 1982; Medved et al. 1985, 1988); stomach contents are usually listed qualitatively (Clark and von Schmidt 1965; Sadowsky 1967; Branstetter 1981). However, frequency of occurrence of shark remains is often 10–15% in those stomachs containing food, especially for certain species such as *Carcharhinus obscurus*, *C. leucas*, and *Galeocerdo cuvieri* (see Bass et al. 1973 for an excellent summary).

Additionally, the smaller the shark, the more vulnerable it is to such predatory risk. Off Brazil, the most common sharks noted in the stomach contents of seven species of sharks were neonatal or young *Carcharhinus porosus*, *Sphyrna lewini*, *S. tiburo*, and young and adult *Rhizoprionodon porosus*, and *R. lalandei*; even adults of the intermediate sized *C. porosus* (L_{max} ~140 cm) fed on neonatal *S. lewini* and *R. lalandei* (Sadowsky 1967). All of these prey species are relatively small sharks.

One of the important predatory shark species is the bull shark, *Carcharhinus leucas*, which has been reported to feed on small *C. limbatus*, *C. acronotus*, *C. isodon*, *C. plumbeus*, and *C. porosus* (Springer 1960, 1963, 1967; Tuma 1976; Sadowsky 1967, 1971; Snelson et al. 1984). Springer (1960) suggested the bull shark was a major source of mortality on young sandbar sharks, *C. plumbeus*, and Sadowsky (1971) noted that even young (adolescent?) bull sharks preyed on small sharks, including neonatal *Sphyrna tiburo*.

Such predatory risk is reduced for many species by the use of nursery grounds for the young. These nursery grounds serve a two-fold purpose: by segregating the young from the adult populations they offer protection from predation and they usually have numerous prey items for the pups. The nursery grounds can be categorized by their degree of exposure to potential predators. Some are "protected," because they are in areas infrequently inhabited by adult sharks, while others are very "unprotected," because they are located in habitats occupied by adults.

Additionally, the speed at which maturity is attained may also contribute to cohort strength and recruitment. Small species, such as *Rhizopriondon terraenovae*, mature more quickly and reproduce more often than larger species such as the bull shark, *Carcharhinus leucas* (Parsons 1985; Branstetter 1987a, Branstetter and Stiles 1987).

Hoenig and Gruber (1990) discuss the importance of several biological parameters related to management purposes. Data are now available for many of these characteristics (see Pratt 1990 and Cailliet 1990 for a review), and based on such data, I have categorized the species into groups with similar life-history characteristics (Table 1). Given the restrictions of viviparity as outlined earlier, a female can produce either a few, large young, or numerous, small young. For the shark species considered here, both options occur: the production of relatively few young (<15; usually 6–8) that, at birth, are >20% of the maximum adult size (L_{max}) (total lengths are used throughout this report), or the production of more numerous young (30–70) at <20% L_{max}. It should be pointed out that these are minimal values as most adults are smaller than L_{max}; the average female *Rhizoprionodon terraenovae* is ~95 cm, with L_{max} = 110 cm. These two groups must be further subdivided by the actual size of the pups because size terminology here is relative. For example, the small (L_{max} 110 cm) Atlantic sharpnose shark produces pups that are 30–35 cm at birth. This is a large pup compared to the mother (~ 30% L_{max}), but small compared to the size at birth for larger species or to potential predators. For this discussion, I have distinguished two categories: small pups (<70 cm at birth) and large pups (>70 cm at birth).

Growth data are now available for many species. For this discussion, growth rates are categorized by the Brody growth coefficient K (Ricker 1975) and have been separated at the value of < or >0.10. Several species have estimated K values of >0.20; with future data on additional species, further subdivisions might be beneficial. However, K values, although providing a comparative constant for overall life history, may not adequately represent early

Table 1.

Species groups of selected carcharhinoid and lamnoid sharks of the northwestern Atlantic based on life history characteristics. Lengths and growth expressed as cm TL. BL = birth length. K represents the Brody growth coefficient. See citations in the text for data sources for each species.

Birth >20% L_{max}

K <0.10; <30% BL						K >0.10; >40% BL					
Species	L_{max}	Birthsize (% L_{max})	No. young	Yr. 1 growth (% BL)	K	Species	L_{max}	Birthsize (% L_{max})	No. young	Yr. 1 growth (% BL)	K
Coastal											
Small young											
C. leucas	300	70(23%)	6–10	15(22%)	0.07	*R. terraenovae*	110	32(29%)	6–8	22(69%)	0.35–0.50
C. plumbeus	250	65(26%)	6–10	15(23%)	0.05	*S. tiburo*	120	30(25%)	6–8	20(67%)	0.34–0.58
N. brevirostris	300	65(22%)	6–18	15(23%)	0.05	*C. porosus*	134	30(22%)	6	?	?
						C. isodon	160	50(31%)	6–8	25(50%)	0.10–0.22
						C. acronotus	165	45(27%)	4–6	17(38%)	0.13
						C. limbatus	200	55(27%)	6–10	35(65%)	0.20–0.27
						C. brevipinna	240	65(27%)	6–10	40(62%)	0.22
Large young											
O. taurus	300+	100+(33%)	2	30(30%)	0.07–0.09						
Pelagic											
Small young											
C. longimanus	275+	65(24%)	10–15	20(30%)	0.04–0.09	*C. signatus*	275+	65(26%)	10–18	32(50%)	0.10–0.15
						C. falciformis	310	70(23%)	10–15	45(65%)	0.15
						L. nasus	270	70(26%)	2	35(45%)	0.11
						I. oxyrinchus	375	70+(20%)	8–10	40(57%)	0.20–0.27
						A. superciliosus	400	100(25%) [55 PCL]	2	40(36%)	0.30?
Large young											
C. obscurus	360	90(25%)	10–12	15(16%)	0.07	*I. paucus*	420	110(26%)	2	40(40%)	0.10–0.20?
C. carcharias	650	140(22%)	8–10	40(30%)	0.06	*A. vulpinus*	650	140(22%) [75+ PCL]	2	40(28%) [40(55%)]	0.11–0.21

? ⟵ *C. perezi*

C. brachyurus ⟶ ?

? ⟵ *C. altimus*

? ⟵ *C. galapagensis*

Birth <20% L_{max}

K <0.10; <30% BL						K >0.10; >40% BL					
Species	L_{max}	Birthsize (% L_{max})	No. young	Yr. 1 growth (% BL)	K	Species	L_{max}	Birthsize (% L_{max})	No. young	Yr. 1 growth (% BL)	K
Coastal											
Small young											
S. mokarran	560	70(13%)	30–40	?	?	*G. cuvieri*	450	70(16%)	30–70	70(100%)	0.11–0.18
S. lewini	310	45(15%)	30–40	17(38%)	0.07						
Pelagic											
Small young											
S. zygaena	390	50(13%)	20–40	?	?	*P. glauca*	350	45(13%)	40–80	40(90%)	0.11–0.25
Large young											
C. carcharias	760	140(18%)	8–10	40(30%)	0.06						

growth and attainment of minimum sizes as considered in this discussion. Therefore, early growth is also discussed as a ratio of the first year's growth compared to the length at birth (BL). As an example, the Atlantic sharpnose shark is born at ∼32 cm and increases ∼22 cm in length during its first year (Parsons 1985; Branstetter 1987a), for a first years' growth of 69% BL. This is rapid growth, but the shark is still relatively small compared to potential predators. A one year old sharpnose shark is still smaller than a neonatal *Carcharhinus limbatus*.

Several important characteristics such as recruitment and survival/mortality, especially in relation to their early life history, are still poorly understood (Hoff and Musick 1990). Although it is probably impossible, at present, to make accurate estimates of these parameters, this paper attempts to draw on the known characters to make some inferences about the early life history of species that may help answer some of the remaining questions.

Species with Slow Growth ($K < 0.1$; <30% BL)

This group is divided according to the size of the newborns and the kind of nursery ground they use: 1) exceptionally large (~100 cm) young that occupy coastal and surf areas that expose them to predators, or 2) smaller (<70 cm) young that use bays and estuarine areas as nursery grounds, thus avoiding potential predators. This group can be further subdivided by the relative size of the young compared to the adults (see Table 1), but the two primary categories are adequate for this discussion.

Species with Large Neonates

The sand tiger, *Odontaspis taurus*, is a common, large coastal shark of warm-temperate regions, reaching a maximum size of >300 cm (Springer 1960; Gilmore et al. 1983). The embryos are oviphagous and cannibalistic during development; therefore, only two extremely large (>100 cm) young (Gilmore et al. 1983) are generally produced. Nursery grounds are littoral, temperate waters, but do not include embayments or low salinity areas (Bass et al. 1975b); thus, the young are exposed to predation by the abundant adult sharks of these areas. Age and growth data are lacking for this species except for captive specimens discussed in Gilmore et al. (1983), but using their length at age data in Ford/Walford plots (Ricker 1975) I calculated a K value of 0.07–0.09. First year growth was ~30% BL under these optimal environmental conditions. Even if the actual growth rate is slower, first year growth coupled with the initial large size of the pups should decrease predatory risks on the young.

Similarly, the dusky shark, *Carcharhinus obscurus*, a large ($L_{\max}$ 360 cm: Garrick 1982) common shark of continental shelf and insular regions, gives birth to young at a relatively large size (80–100 cm) (Clark and von Schmidt 1965; Bass et al. 1973; Branstetter 1981; Compagno 1984). Nursery grounds appear to be surf zone areas, but do not include embayments or lowered salinity areas (Bass et al. 1973). As with *Odontaspis taurus*, the large size of neonates may reduce predation by the adults of the common coastal sharks. However, the 10–15 young produced in each litter (Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981) suggest that mortality rates on these young may be high. Bass et al. (1973) listed *C. obscurus* pups as a food item of *C. limbatus*, and *O. taurus* is also known to prey on the *C. obscurus* pups (J. Musick, Virginia Inst. Mar. Sci., Gloucester Point, VA, 23062, pers. comm., 1988). The pups grow slowly, only about 15 cm/yr (16% BL; K = 0.07, calculated from data of Schwartz 1983), but the pups would be >100 cm by one year of age. Again, attainment of this size may reduce mortality rates.

A third variation of this pattern is exemplified by the white shark, *Carcharodon carcharias*. This species is known to attain a length of 600 cm, and is estimated to reach a maximum size of >760 cm (Cailliet et al. 1985). Unlike most lamnoids which produce 2–4 young, the white shark produces 8–10 young per litter (Randall 1973; S. Uchida, Okinawa Aquarium, Okinawa, Japan, pers. comm., Dec. 1987), at approximately 140 cm (Stevens 1984; Cailliet et al. 1985). Although these are large pups, they are small compared to the adults (approximately 18% $L_{\max}$). Based on the capture localities of young (Cailliet et al. 1985; Casey and Pratt 1985), birth probably occurs in neritic or pelagic cool temperate waters. The pups grow ~30% BL (K = 0.06: Cailliet et al. 1985; Welden et al. 1987) their first year, and would be larger than most potential predators. Randall (1987) presented evidence refuting several length records of the white shark (>640 cm). Should their maximum size be near 650 cm instead of the 760 cm estimated by Cailliet et al. (1985), they would need to be categorized in Table 1 with *Carcharhinus obscurus* (birth >20% $L_{\max}$, $K < 0.1$, <30% BL).

Species with Small Neonates

Three species in this group have very similar patterns. The bull shark, *Carcharhinus leucas*, and the sandbar shark, *C. plumbeus*, are common in warm temperate coastal waters, and the lemon shark, *Negaprion brevirostris*, is more common in tropical environments. *C. leucas* reaches a maximum size of ~300 cm (Sadowsky 1971; Garrick 1982; Branstetter and Stiles 1987), *C. plumbeus* a maximum size near 250 cm (Springer 1960; Casey et al. 1985), and both produce 6–10 young 60–70 cm in length (Springer 1960; Clark and von Schmidt 1965; Branstetter and Stiles 1987), although some *C. leucas* pups develop to extraordinary size (75–85 cm) at the expense of their intra-uterine litter mates (Sadowsky 1971; Dodrill 1977; Branstetter and Stiles 1987).

Both *C. leucas* and *C. plumbeus* pups grow slowly (*C. leucas*—K = 0.07: Thorson and Lacy 1982; Branstetter and Stiles 1987; *C. plumbeus*—K = 0.05: Casey et al. 1985), increasing in length approximately 15 cm/yr (22% BL for *C. leucas*, 23% BL for *C. plumbeus*). *C. leucas* uses bays and estuaries of the Gulf of Mexico and the east coast of Florida as nurseries and the pups penetrate freshwater areas (Caillouet et al. 1969; Dodrill 1977; Branstetter 1981; Snelson and Williams 1981; Snelson et al. 1984) as they do in other parts of their range (Bass et al. 1973; Thorson and Lacy 1982). *C. plumbeus* pups occupy the lower portions of bays and sounds (Branstetter 1981; Casey et al. 1985).

Both species frequent estuaries for several years. In the fall of their first year, the pups are ~85 cm (Snelson et al.

1984; Casey et al. 1985), and they move offshore to overwinter at the continental shelf edge (Springer 1960; Branstetter 1986). They return again to the bays the next spring; juveniles of a size corresponding to one-year-old sharks are common in estuarine areas (Caillouet et al. 1969; Sadowsky 1971; Branstetter 1981; Casey et al. 1985). At lengths of ~120 cm for *C. plumbeus* and 130 cm for *C. leucas* (Sadowsky 1971; Casey et al. 1985; Branstetter and Stiles 1987) both species begin occupying primarily continental shelf waters. At this length they are large enough to avoid predation because of both their size and speed.

In warm temperate regions, *Negaprion brevirostris* has a similar early life history to the bull and sandbar sharks, however the species is not as common in these regions. More commonly found in tropical regions, this large shark ($L_{\max}$ 300 cm: Springer 1950a, 1960; Clark and von Schmidt 1965) gives birth to pups 60–70 cm in length. The pups occupy shallow coral reef flats as a nursery ground (Clark and von Schmidt 1965; Gruber 1981, 1982; Gruber and Stout 1983), and grow ~15 cm/yr (20–25% BL) (K = 0.05 following data of Gruber and Stout 1983). The shallow reef flats offer protection for these juveniles, although predation by adults of their own species and other large sharks may result in a 50% mortality rate (S. Gruber, RSMAS, Univ. Miami, 33149, pers. commun., June 1987). Litters of 8–18 ($\bar{x}$ = 12) pups (Clark and von Schmidt 1965) may help offset this mortality rate.

The protected nursery area strategy is varied slightly by the scalloped hammerhead, *Sphyrna lewini*. This species attains a length >300 cm and, as an adult, occupies offshore waters more commonly than coastal waters (Clarke 1971; Klimley 1981; Branstetter 1987b). The species produces numerous small young (>30/litter) at 40–50 cm, which occupy bays, sounds, and beach front areas as a nursery (Sadowsky 1965; Clarke 1971; Bass et al. 1975a; Dodrill 1977; Snelson and Williams 1981; Branstetter 1987b). These young grow ~15 cm in the first six months, and 15 cm/yr for the next two years (K = 0.07: Schwartz 1983; Branstetter 1987b). (This growth rate is 38% BL, which is a larger value than the category in which they are placed [<30% BL], but it is still much slower than most of the rapid-growing species with growth rates >50% BL). Instead of remaining in the protected nurseries, the pups move into littoral regions after the first three months where they are exposed to predation (Sadowsky 1967; Clarke 1971; Snelson and Williams 1981; Branstetter 1987b). *Sphyrna lewini* pups were the most common shark in stomach contents listed by Sadowsky (1967), and Clarke (1971) noted they were preyed upon heavily by adult males of their own species in Hawaii. This apparent high mortality rate among cohorts may be compensated for by the large litter size.

Similarly, the oceanic whitetip shark, *Carcharhinus longimanus*, ($L_{\max}$ 270–300 cm: Bass et al. 1973) is an offshore species that gives birth to relatively large litters (12–16 pups) at a small size, about 65 cm (Backus et al. 1956; Garrick 1982; Stevens 1984). Limited age/length data (Saika and Yoshimura 1985) suggest this species grows slowly; juvenile growth is about 20 cm/yr (30% BL) (K = 0.04–0.09: from data in Saika and Yoshimura 1985), therefore the pups, born in oceanic tropical waters, are more vulnerable to predation, except that few species occupy such water, although those that do are relatively abundant. Attainment of a size that would deter predation may require two to three years. The larger litter size may offset this longer vulnerability to such predatory risk.

The overall biology of the great hammerhead, *Sphyrna mokarran*, and the smooth hammerhead, *S. zygaena*, are poorly understood. However, available data (Clark and von Schmidt 1965; Sadowsky 1965, 1971; Bass et al. 1975a; Castro 1983; Stevens 1984) indicate their life histories are similar to that of S. *lewini*, and for the time being, they are included in this group. They both produce large numbers of young (20–40) after approximately a one-year gestation period. *S. mokarran* pups are born at 70 cm (13% $L_{\max}$), and are taken along beach areas (Dodrill 1977; Branstetter, unpubl. data). Growth may be similar to that of *S. lewini* (Branstetter, unpubl. data). Little is known of the biology of *S. zygaena*; pups are born at ~50 cm (13% $L_{\max}$), and may occupy a more oceanic zone.

Species with Fast Growth (K >0.1; >40% BL)

This category contains the majority of species under consideration in this review. It also contains a wide range of sharks; small sharks that reach a maximum size of approximately 100 cm to large species that attain in excess of 300 cm maximum length. Nursery grounds for the pups of these species tend to be exposed to predators to varying degrees. Cohort survival appears to be more dependent on cohort strength and growth rate than on occupation of a protected nursery ground. As with slow-growing species, attainment of a size that both deters predation and increases swimming efficiency appears to be an important survival factor. The species in this group can be divided between coastal and pelagic species with the coastal group further subdivided by the size attained by the species.

Small ($L_{\max}$ ~100 cm) Coastal Sharks

This group includes the sharpnose sharks, *Rhizoprionodon* spp., the bonnethead, *Sphyrna tiburo*, the smalltail shark, *Carcharhinus porosus*, and certain traits of this group are applicable to intermediate-sized species such as the finetooth shark, *C. isodon*, and the blacknose shark, *C. acronotus*. The well studied Atlantic sharpnose shark, *R. terraenovae*, (Parsons 1983a, 1983b, 1985; Branstetter 1981, 1987a) is a good example of the strategy followed by this group. The species occurs in warm temperate waters of the southeastern United States and is the most common shark taken in the Gulf of Mexico (Cody et al. 1981; Branstetter 1981, 1986). This small shark (<110 cm) is probably vulnerable to predation throughout its life history. Adult *R. porosus* and *R. lalandei* are common food items of larger sharks (Sadowsky 1967). It grows comparatively fast (69% BL) ($K = 0.35$–0.50: Parsons 1985; Branstetter 1987a) with males reaching maturity in three years, females in four years. In areas where reproduction occurs, catch rates for females outnumber males in the adult population 3:1 (Branstetter 1981; Parsons 1983b). Females give birth to 4–6 young annually; there is no resting stage in the female reproductive cycle as is common in larger carcharhinids (Pratt 1979; Branstetter 1981; Parsons 1983b). The pups, although small at birth (30–35 cm), are large compared to the size of the mother (29% of $L_{\max}$). Nursery grounds are littoral zones, including beach and surf areas. The young also occur in the mouths of bays and coastal sounds, possibly migrating with tidal fluctuations (Parsons 1983b; Branstetter 1986, 1987a). Adults of several shark species occupy these littoral zones, and mortality of newborns should be significant. In other areas neonatal *R. porosus* and *R. lalandei* are common food of larger sharks (Sadowsky 1967). Adequate adult recruitment may be dependent on large annual cohorts and rapid maturation. This is suggested by 1) the possible domination of females in reproductively active populations, 2) an annual reproductive cycle without a resting stage, and 3) the production of numerous young as large as can be accommodated in the female body cavity. Parsons (1983b) suggested that females that produce fewer, larger young may be the most efficient.

Similarly, the life history of the bonnethead, *Sphyrna tiburo*, recently described by Parsons (1987) suggests it may suffer from a higher mortality because of its small size. This shark, reaching a maximum length of 120 cm, grows rapidly ($K = 0.34$–0.58) maturing in about two years, and produces 6–9 young a year. The reproductive cycle is very short, 4–5 months, and the pups are born at 25–35 cm depending on locality and environmental factors. Pup growth is rapid, 20+ cm/yr (67–80% BL). The pups are found in bays and coastal waters, where they are often preyed upon by larger sharks (see Introduction) (Sadowsky 1967).

Little is known about *C. porosus*. It reaches a maximum size of ~140 cm, and produces <10 young per litter. Its size and general habitat preference suggest it is similar to the other species (Garrick 1982; Compagno 1984; J. Castro, Clemson Univ., SC 29631, pers. commun., Nov. 1988).

Large ($L_{\max}$ >150 cm) Coastal Sharks

Life histories for medium-sized species such as *Carcharhinus isodon* ($L_{\max} = 160$ cm: Springer 1950b; Branstetter and Shipp 1980) and *C. acronotus* ($L_{\max} = 165$ cm: Schwartz 1984) are intermediate between the small species and larger coastal sharks. The female reproductive cycle has a one year resting stage similar to larger sharks, but the young (4–6/litter) are relatively small at birth (45 cm for *C. acronotus* and 50 cm for *C. isodon* [Branstetter and Shipp 1980; Branstetter 1981; Schwartz 1984]). They occupy littoral zones where they are exposed to predation from the abundant coastal sharks. Both species grow at a moderate rate; neonates increase approximately 20 cm in their first year (~50% BL for both species) (*C. acronotus*—$K = 0.13$: Schwartz 1984; *C. isodon*—$K = 0.10$–0.22 Branstetter, unpubl. data). Pups of both species are known prey items of the bull shark. As with the smaller sharks, an earlier maturation may help offset mortality rates.

The two common species in the category, the blacktip shark, *Carcharhinus limbatus*, and the spinner shark, *C. brevipinna*, have similar life history patterns (Clark and von Schmidt 1965; Branstetter 1981, 1987c). These two species comprise 1/3 to 1/2 of the catch of epipelagic coastal sharks taken on longlines in the Gulf of Mexico (Branstetter 1987c). In the northwestern Atlantic region both species reach a maximum size of >200 cm, with *C. brevipinna* being the larger of the two, reaching 240 cm. Both produce 6–10 young after a 12 month gestation period in a two-year reproductive cycle. *C. limbatus* pups are born at 50–60 cm, and *C. brevipinna* pups are born at 60–70 cm (Branstetter 1981, 1987c). Both use the relatively unprotected littoral zones as nurseries, and pups invade lower portions of bays and sounds with the tide, but neither penetrate low salinity areas (Snelson and Williams 1981; Branstetter 1987c).

Growth for both species is relatively fast: *C. limbatus*—$K = 0.20$–0.27; *C. brevipinna*—$K = 0.22$ (Killam 1987; Branstetter 1987c). Pups increase >20 cm in the first six months of life. They apparently continue to grow through the first winter after they move offshore to deep regions of the outer continental shelf. When they return to coastal waters in the spring, they have attained lengths in excess of 90 cm for *C. limbatus* (85% BL) and 100 cm for *C. brevipinna* (67% BL). These one-year-old sharks are common in littoral zones. Growth continues at 15–20 cm/yr through the second year, thus they attain a size that may deter predators, and allow them to attain swimming speeds to actively avoid predation.

Pelagic Species

Similar to coastal carcharhinids, the silky shark, *C. falciformis*, apparently depends on rapid growth for adequate neonate survival. In the central Pacific, Strasburg (1958) noted the silky shark was twice as abundant in neritic waters compared to open ocean situations, and in the Gulf of Mexico the species is more common along the edge of the continental shelf (150–500 m) (Branstetter 1987b). This large (>300 cm) cosmopolitan epipelagic shark gives birth to 6–14 young at 70–75 cm (Strasburg 1958; Bane 1966; Bass et al. 1973; Cadenat and Blache 1981; Branstetter 1987b). In the tropics, this shark may not have a seasonal gestation period (Strasburg 1958; Bane 1966; Stevens 1984), but in the warm-temperate Gulf of Mexico, it appears to give birth in summer (June–August) (Branstetter 1987b). Springer (1967) suggested that neonates inhabit deep reef areas along the continental shelf edge, but apparently they move to a pelagic existence by the first winter (6 months of age) (Branstetter 1987b). Their size at birth makes the pups vulnerable to predation from the large epipelagic sharks of the region. Cohort survival appears to be enhanced by rapid growth ($K = 0.15$) and schooling behavior (Branstetter 1987b). The pups increase 25–30 cm in length by the first winter, and are approximately 115 cm by 1 year of age (65% BL). Neonates are taken on pelagic longlines during the winter in the Gulf of Mexico (Branstetter 1981, 1987b), separate from the subadult and adult part of the population. Yoshimura and Kawasaki (1985) also noted juvenile silky sharks in the western central Pacific tended to aggregate by size.

Another pelagic carcharhinid, the night shark, *Carcharhinus signatus*, may have a similar early life history. This species occurs in deep waters along the edge of the continental shelf on both sides of the Atlantic and may be most abundant in the Florida Straits (Raschi et al. 1982; Garrick 1985; Branstetter and McEachran 1986a). *C. signatus* reaches a maximum size near 275 cm, and gives birth to 12–18 pups at 60–70 cm (Branstetter 1981, 1986; Garrick 1985). These pups occupy the epipelagic zone along the continental shelf edge where they are exposed to predators. Accurate age and growth data are lacking for this species, but preliminary data indicate the pups grow 30–35 cm/yr (50% BL) ($K = 0.10–0.15$ following data in Branstetter 1986), attaining a length in excess of 100 cm in a little over a year, similar to that of the silky shark.

The pelagic alopiids and lamnids have similar strategies with the young being dependent on size for survival. Most lamnoids produce 2–4 large (~100 cm) young (Bass et al. 1975b; Gruber and Compagno 1981; Otake and Mizue 1981; Gilmore 1983), but the shortfin mako, *Isurus oxyrinchus*, (L_{max} 375 cm: Pratt and Casey 1983) produces numerous young (6–18) that are comparatively smaller (70+ cm) (Gohar and Mazhar 1964; Gubanov 1972, 1978; Stevens 1983, 1984; Branstetter 1981, unpubl. data). The size of neonate *I. oxyrinchus* makes them more vulnerable to predators, but the larger litter size may offset this mortality rate. In the northwestern Atlantic the population has a relatively fast growth rate with juveniles increasing approximately 40 cm/yr (57% BL) for the first two years ($K = 0.203–0.266$: Pratt and Casey 1983). Such rapid length-increases and associated increased swimming efficiency and speed should reduce predatory risks.

In contrast, the much larger (L_{max} >420 cm: Gilmore 1983) longfin mako, *I. paucus*, a tropical mesopelagic species that rarely enters continental shelf waters (Dodrill and Gilmore 1979; Killam and Parsons 1986) gives birth to two young at >100 cm (Gilmore 1983). As with other offshore pelagic sharks, a nursery ground, per se, may not be used; females probably give birth in open ocean waters, and the pups remain in pelagic waters. The young are of a size that should deter predators and allow them to attain swimming speeds necessary to actively avoid predation (Gilmore 1983). Growth rates are unknown, but Branstetter (1986) reported similar numbers of vertebral bands in similar sized *I. oxyrinchus* and *I. paucus*, suggesting they have similar growth rates (40 cm/yr); growth through the first year would be near 40% BL.

The porbeagle, *Lamna nasus* (L_{max} 260–280 cm: Aasen 1963), also gives birth to smaller young, similar to *Isurus oxyrinchus* (~70 cm: Aasen 1963), but produces only two or possibly four per litter. Neonates increase to approximately 100 cm (45% BL) in their first year ($K = 0.11$: Aasen 1963). Predation risks may not be as great for the young of this species because few large predators exist in the boreal waters that this species inhabits. An estimated mortality (M) for a virgin stock of this species was approximately 0.18 (Aasen 1963), and much of this can probably be attributed to juvenile mortality.

The alopiids only produce 2–4 young that are of intermediate size at birth. Lengths for this group are difficult to compare because of the exaggerated upper caudal lobe. Although the pups are not large, it is possible that this added size factor could inhibit some predation. The bigeye thresher, *Alopias superciliosus*, which reaches a maximum size near 400 cm (225 cm precaudal length [PCL]) (Gilmore 1983) produces young born at 100–110 cm (55–60 cm PCL) (Bass et al. 1975b; Gruber 1980; Gruber and Compagno 1981; Gilmore 1983), and thresher shark, *A. vulpinus*, (L_{max} 650 cm [325 cm PCL]: Cailliet et al. 1983) young are slightly larger (115–160 cm [65–90 cm PCL]) (Gubanov 1978; Hixon 1979; Cailliet et al. 1983). The third species, the pelagic thresher, *A. pelagicus*, which does not occur in the northwest Atlantic, may also be born at ~100 cm (Otake and Mizue 1981). Little is known of the habits of *A. superciliosus* and *A. pelagicus* young, but the juveniles are taken on longlines in open ocean pelagic waters. Their size, coupled with a relatively rapid growth rate may be adequate for survival (Gilmore 1983). Gruber and Compagno (1981) estimated growth for newborn *A. superciliosus* at ~40 cm/yr (36% BL). On the basis of their data I calculated a K of 0.3, but Gruber and Compagno warned that their growth estimates were only first order approximations. *A. vulpinus* is associated more with continental shelf waters, especially the young (Bass et al. 1975b; Gubanov 1978; Branstetter 1981; Cailliet et al. 1983). These waters are occupied by numerous carcharhinid and lamnid sharks, thus the young are exposed to greater predatory pressures than their oceanic congeners. Their larger size at birth and rapid juvenile growth (K = 0.11–0.21: Cailliet et al. 1983; Cailliet and Bedford 1983; Cailliet and Radtke 1987) of 40 cm/yr (>25% BL) may offset such predation.

Rapid Growth, Large Litters

The last two species to be considered here also have rapid growth rates but produce comparatively large numbers of young; this fact suggests that mortality rates on the young may be high compared to other species. The blue shark, *Prionace glauca*, is one the most common offshore pelagic sharks of temperate and tropical waters (Strasburg 1958; Stevens 1984), reaching a size of at least 350 cm (Pratt 1979; Cailliet and Bedford 1983; Compagno 1984). *P. glauca* gives birth to numerous (40–80), small (40–50 cm) young in epipelagic oceanic waters (Pratt 1979; Stevens 1984), similar to the lamnoids. However, their small size suggests they are vulnerable to predation. Little is known of blue shark early life history, but growth studies for the Atlantic population (K = 0.13: Aasen 1966; K = 0.11: Stevens 1975, 1976) and the Pacific population (K = 0.17–0.25: Cailliet et al. 1983; Cailliet and Bedford 1983) indicate neonates nearly double in length (40 cm/yr) their first year (90% BL). During the second year they grow approximately 30 cm, with growth gradually decreasing through maturity. Even with a rapid growth rate, mortality may be high on young cohorts as suggested by the litter size.

The tiger shark, *Galeocerdo cuvieri*, also grows extremely fast in early life (K = 0.11–0.18: Branstetter et al. 1987). This species, reaching a maximum length of 400–450 cm, gives birth to numerous (40–70) young that are small (70 cm) compared to the adults (Kauffman 1950; Bass et al. 1975a; Branstetter 1981; Branstetter et al. 1987). Specific nursery areas are unknown, but the young are born in coastal waters that expose them to predation by the abundant coastal species, including their own. At birth, they are extremely long and slender and produce an inefficient anguilliform-type swimming motion, and the caudal fin has a low thrust angle (Thompson and Simanek 1977), thus precluding a rapid swimming speed. Neonates grow rapidly, doubling in length the first year of life (100% BL) to ~140 cm (Clark and von Schmidt 1965; Branstetter et al. 1987). Rapid linear growth (30 cm/yr) continues for the next two years until the sharks exceed 200 cm in length. Throughout this period they remain relatively slender-bodied, but swimming efficiency may increase through increased body rigidity and increased caudal fin thrust angle. At 200 cm, linear growth begins to decline, and the rate of weight gain increases, but by this time, they are larger than most potential predators and probably are predators on younger sharks themselves.

Conclusions

Shark species vary several life-history characteristics to provide for adequate cohort survival. The attainment of approximately 100 cm TL may be a critical factor in neonate survival as they are then large enough to deter many predators as well as active enough to avoid predation by means of increased swimming speed and efficiency. This may be accomplished by two different strategies: 1) rapid growth in nursery grounds exposed to predators, or 2) slow growth in protected nursery grounds. Small species which are nearing their maximum size at 100 cm are probably susceptible to predation throughout their life history and offset this higher mortality rate with a higher fecundity.

From the categories in Table 1, 14 of the 26 species have a relatively similar strategy—the production of small numbers of offspring that are fairly large in relation to size of the mother (birth length >25% $L_{\max}$). These young then grow relatively rapidly, increasing 40–80% of the birth length in their first year. However, this category covers a wide group of sharks from the small, coastal Atlantic sharpnose shark to the large, pelagic shortfin mako. Obviously there are some significant differences in the overall life histories of the individual species within this category. The remaining 12 species have evolved similarly successful strategies but have placed emphasis on different life history characteristics.

Very few species, or stocks, have been investigated extensively enough to estimate mortality rates, especially age specific mortality, however it can be assumed that predation on juveniles probably constitutes a major source of overall mortality on the populations. Because viviparous sharks have a limited uterine space available for embryo development, there is an inverse relationship between the number and size of young produced. With the general slow growth and late maturation exhibited by viviparous sharks (see Cailliet et al. 1986 and Cailliet 1990 for a review) such a reproductive strategy results in a direct relationship between stock and recruitment. Thus sharks, as a group, are extremely susceptible to overfishing (Holden 1974, 1977). The increasing exploitation of adult stocks may result in reduced future cohort strength, leading to insufficient recruitment, and eventual collapse of populations. Because of the multispecies nature of the developing shark fishery, management at the group level will be desirable but difficult to achieve owing to the variations in the life history strategies employed by the different species (Branstetter and McEachran 1986b).

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Diet, Feeding Habits, Digestion, and Consumption in Sharks, with Special Reference to the Lemon Shark, *Negaprion brevirostris*

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ABSTRACT

Though the diets of many species of sharks have been described, little information exists about patterns of food intake and about the fate of prey items once they are ingested. Digestive physiology and efficiency of elasmobranchs are generally accepted as similar to those of teleosts, although digestive morphologies of the two groups differ. The lemon shark, *Negaprion brevirostris*, has been the subject of a series of studies examining characteristics of consumption and digestive processing of food. Diet of young lemon sharks and many other sharks is dominated by teleosts. Feeding by lemon sharks is asynchronous, intermittent, and exhibits no pattern of periodicity. A meal is completely evacuated from the stomach of lemon sharks 25–41 hours after feeding, depending on meal type and temperature. Fecal production continues for 68–82 hours after feeding in the lemon shark. A relatively long period of time is also required for digestive processing of food in other species of sharks. Lemon sharks absorb energy from food with an efficiency similar to that of most teleosts. Daily ration has been estimated at 1.5–2.1% body weight/day, which is intermediate in comparison to estimates for other species of sharks and which is low in comparison to most teleosts. Lemon sharks are able to convert ingested energy to energy stored as growth as efficiently as many teleosts. Slow rates of digestion and consumption are factors which probably limit growth in the lemon shark and other elasmobranchs. Our findings for the lemon shark are compared with information gathered for other species of sharks.

Introduction

Sharks are one of the most abundant apex predators in the sea, playing a major role in the exchange of energy between upper trophic levels of the marine environment. Yet studies of consumption and feeding ecology of sharks are few, and knowledge of their role in the marine ecosystem is very limited. Although there are numerous lists of food items found in the stomachs of sharks (Baughman and Springer 1950; Clark and von Schmidt 1965; Randall 1967; Dahlberg and Heard 1969), there have been very few quantitative reports of various prey and fewer estimates of the amount of food consumed on an annual or daily basis. There are also few descriptions of feeding behavior or activity patterns associated with prey selectivity of predatory sharks. In addition there is little information on digestive processes or the efficiency with which energy is absorbed and converted to growth.

The lemon shark (*Negaprion brevirostris*), which ranges from New Jersey to Brazil, is particularly abundant off Florida and in waters of the Bahamas (Springer 1950; Compagno 1984), and may represent an important energy sink in these areas of local abundance. To more fully define the role of the lemon shark in the tropical marine environment, we have been studying many factors, including diet, feeding habits, digestive physiology, growth, and other energetic parameters of this species. The following is a review of our observations about what, when, how much, how often and how efficiently lemon sharks eat; and what happens to food once it is ingested. These findings are then compared with information available for other species of sharks, and a synthesis is attempted.

Table 1.
Teleost prey in the stomachs of sharks.

Species	% occurrence of[a] teleosts in stomachs	Reference
Prionace glauca	90	Stevens 1973
Carcharhinus leucas	86	Tuma 1976
C. leucas	80	Snelson et al. 1984
Triaenodon obesus	78	Randall 1977
P. glauca	75	Tricas 1979
Negaprion brevirostris	71	Cortes and Gruber, In press
Sphyrna lewini	68	Clarke 1971
Isurus oxyrinchus	67	Stillwell and Kohler 1982
Carcharhinus plumbeus	37	Medved et al. 1985
	% contribution of[b] teleosts in stomachs	
N. brevirostris	88	Schmidt 1986
N. brevirostris	74	Cortes 1987
Squalus acanthias	74	Bowman 1986
Dalatias licha	71	Matallanas 1982
S. acanthias	55	Jones and Geen 1977
Triakis semifasciata	50	Talent 1976
Scyliorhinus canicula	3–6	Lyle 1983

[a] Percentage occurrence of teleosts = stomachs containing teleosts/stomachs sampled.

[b] Percentage contribution of teleosts based on weight, volume, or index of relative importance.

Diet

The impact of sharks on a particular trophic level may be determined by knowing the amount and diversity of prey consumed. Sharks are abundant, wide ranging, and some compete with man by consuming commercially important species. Studies of the diets of sharks have been useful in evaluating the degree of predation on certain fish stocks and the level of competition with man. For example, fishermen accused the spiny dogfish, *Squalus acanthias*, of preying upon herring and young salmon to an extent that they represented a real competition to commercial and recreational fisheries (Ketchen 1975). However, until a quantitative study of the diet of these sharks was conducted (Jones and Geen 1977), there was little basis for refuting such claims.

The importance of teleosts in the diet of sharks is demonstrated by their prominence in the stomachs of many species of sharks (Table 1). Cortes and Gruber (In press) investigated the diet of the lemon shark by examining stomach contents of sharks caught with monofilament gill nets or set line off the Bahamas and Florida Keys. In three such studies, teleosts were the dominant prey items, accounting for 74% of stomach contents on the basis of relative importance. In a limited study, Schmidt (1986) noted that teleosts contributed 88% of the diet of lemon sharks caught in Florida Bay.

Nonteleosts (not including marine mammals or elasmobranchs) form about 10% of the diet of young lemon sharks, but appear to be more important in other species of sharks, and may even dominate the diet of some sharks (Table 2). For example, young leopard sharks, *Triakis semifasciata*, and lesser spotted dogfish, *Scyliorhinus canicula*, feed almost exclusively on nonteleost prey, and young sandbar sharks, *Carcharhinus plumbeus*, also feed primarily on crustaceans (Talent 1976; Lyle 1983; Medved et al. 1985).

Marine mammal flesh was not found in the stomachs of lemon sharks, but occurs in the stomachs of other sharks. A few sharks, such as the cookie cutter, *Isistius brasiliensis*; the tiger, *Galeocerdo cuvier*; and the great white, *Carcharodon carcharias*, may be especially adept at feeding upon marine mammals (Jones 1971; Taylor and Naftel 1978; Corkeron et al. 1987). However, the presence of marine mammal flesh in stomachs of other sharks such as the bull, *Carcharhinus leucas*; the Greenland, *Somniosus microcephalus*; the blue, *Prionace glauca*; the mako, *Isurus oxyrinchus*; the sixgill, *Hexanchus griseus*; and the dusky, *Carcharhinus obscurus*, is much less frequent, and may be a result of opportunistic feeding upon dead or dying animals (Bell and Nichols 1921; Templeman 1963; Stevens 1973; Stillwell and Kohler 1982; Ebert 1986; Gruber, pers obs).

Cortes (1987) found that elasmobranchs formed approximately 7% of the diet of larger lemon sharks. Elasmobranchs are especially important in the diet of several

Table 2.
Nonteleost prey in the stomachs of sharks. M = mollusks, CR = crustaceans, R = reptiles, I = variety of invertebrates, and P = polychaetes.

Species	% occurrence of[a] nonteleosts in stomachs	Reference
Prionace glauca	76 M	Tricas 1979
Carcharhinus plumbeus	73 M, CR	Medved et al. 1985
Sphyrna lewini	73 CR	Clarke 1971
Triaenodon obesus	26 M	Randall 1977
P. glauca	25 M	Stevens 1973
Carcharhinus leucas	15 CR, R	Tuma 1976
Isurus oxyrinchus	15 M	Stillwell and Kohler 1982
C. leucas	6 CR	Snelson et al. 1984
	% contribution of[b] nonteleosts in stomachs	
Triakis semifasciata (adult)	99 I	Talent 1976
Scyliorhinus canicula	94–97 CR, M, P	Lyle 1983
T. semifasciata (juvenile)	50 I	Talent 1976
Squalus acanthias	40 CR, M	Jones and Geen 1977
S. acanthias	26 CR, M, P	Bowman 1986
Dalatias licha	12 CR	Matallanas 1982
Negaprion brevirostris	12 CR	Schmidt 1986
N. brevirostris	10 CR, M	Cortes 1987

[a] Percentage occurrence = stomachs containing nonteleosts/stomachs sampled.
[b] Percentage contribution = based on weight, volume, or index of relative importance.

other species of shark, such as the hammerhead, *Sphyrna mokarran*; the bull; the Galapagos, *Carcharhinus galapagensis*; and the tiger shark (Springer 1960; Lineaweaver and Backus 1969; Randall 1977). Other sharks, including the soupfin, *Galeorhinus galeus*; the sandbar; the blue; the kitefin, *Dalatias licha*; the mako; and the sixgill, occasionally feed upon sharks and rays (Olsen 1954; Springer 1960; Stevens 1973; Tricas 1979; Matallanas 1982; Stillwell and Kohler 1982; Ebert 1986).

Hobson (1963) suggested that sharks refrain from feeding on members of their own species, and Tuma (1976) noted that Nicaraguan shark fishermen were reluctant to use shark for bait, because of its relatively low catch rate compared to other bait. Yet Vorenberg (1962) reported that cannibalism could be induced when lemon and bull sharks were excited by the presence of bait. Under natural conditions the lemon shark is cannibalistic. The authors have found small lemon sharks in the stomachs of larger lemon sharks at several locations off the Bahamas and Florida Keys. Budker (1971) states that the cannibalistic tendencies of hammerhead sharks have long been known, and Snelson et al. (1984) described cannibalism in the bull shark.

Springer (1960) concluded that pregnant sharks cease feeding when they enter nursery areas, as a protection measure for the young. Olsen (1984) reached the same conclusion. However, full term pregnant sharks are commonly captured with baited hooks (Clark and von Schmidt 1965; Tuma 1976), and we have regularly observed hooked female lemon sharks giving birth while on the longline in nursery areas at Bimini, Bahamas (Gruber 1988). The preferred bait of these full term females appears to be small sharpnose sharks, *Rhizoprionodon porosus*. Such observations cast doubt upon the theory that pregnant female sharks cease feeding upon entering nurseries for parturition.

A large amount of indigestible material is found in the stomachs of sharks. Plant material accounted for 11% of stomach contents of the lemon shark (Cortes and Gruber, In press). In addition, Schmidt (1986) found plant material in 11% of lemon shark stomachs that he examined. A similar percentage of stomach contents consisted of plant material, mud and stones in the spiny dogfish (Jones and Geen 1977). Plants, stones and other indigestible bottom material have been found in the stomachs of angel, *Squatina* sp.; Port Jackson, *Heterodontus portusjacksoni*; blue; leopard; and mako sharks (Lineaweaver and Backus 1969; McLaughlin and O'Gower 1971; Stevens 1973; Talent 1976; Stillwell and Kohler 1982). Although this plant matter may be of nutritive value, we believe that it is the result of the benthic feeding habits of the sharks.

There are many stories of metallic and indigestible objects recovered from the stomachs of sharks (Lineaweaver and Backus 1969; Budker 1971), or in which sharks have become entrapped (Herz 1940; Bird 1978). Whether these objects are accidentally ingested with prey, or by a shark investigating potential prey, the indiscriminate feeding habits of some sharks is apparent. Moss (1984) suggested that sharks may consume metal objects because they are attracted by their electric field. Tiger sharks are especially renowned for the wide variety of indigestible material found in their stomachs (Lineaweaver and Backus 1969). Baldridge (1982) proposed that tiger sharks ingest indigestible items such as stones or shells as a means of buoyancy control.

Thus, quantitative reports of stomach contents suggest that the diet of most sharks is dominated by teleosts, but nonteleost prey are consumed to a considerable extent by some species. Marine mammals are important in the diet of only a few species of sharks, while elasmobranchs are common in the diet of others, including pregnant females, and cannibalism certainly occurs. Indigestible bottom material is consumed along with prey, and a wide range of indigestible items are found in the stomachs of a few species of sharks.

Feeding Habits

Opportunistic Versus Selective Feeding

We consider an opportunistic feeder as one that generally consumes whatever prey is encountered, rather than one that is selective and ignores available prey for a preferred type. We would expect stomachs of opportunistic feeders to contain a variety of prey, similar in composition and abundance to the prey fauna in the predator's habitat. Stomachs of selective feeders would be expected to contain a predominant prey-type, which in some cases might be less abundant than other prey items in the habitat. However, if a predator were selectively feeding on the most abundant prey, the difference between opportunism and selectivity might be difficult to detect.

Sharks are often considered to eat whatever they happen to encounter. Budker (1971) stated that for a shark to avoid death by starvation it must be in a constant state of readiness, living a life of perpetual ambush, pursuit, and attack, always actively engaged in the search for food. He considered sharks to be such opportunistic feeders that their stomach contents were a good indication of the abundance of marine fauna in a given area. According to Springer (1960), most sharks are opportunistic feeders out of necessity, existing on a feast or famine regimen owing to their ineptness at catching prey. Springer (1967) found no indication that the kind of internal drive that man knows as hunger operates or even exists for sharks. Such reports reflect the opinion held by many, but much more information has recently been gathered on feeding habits of sharks, providing evidence for a very different view. Some species of sharks indeed appear to be opportunistic, but the extent to which they are opportunistic or selective feeders is not well defined.

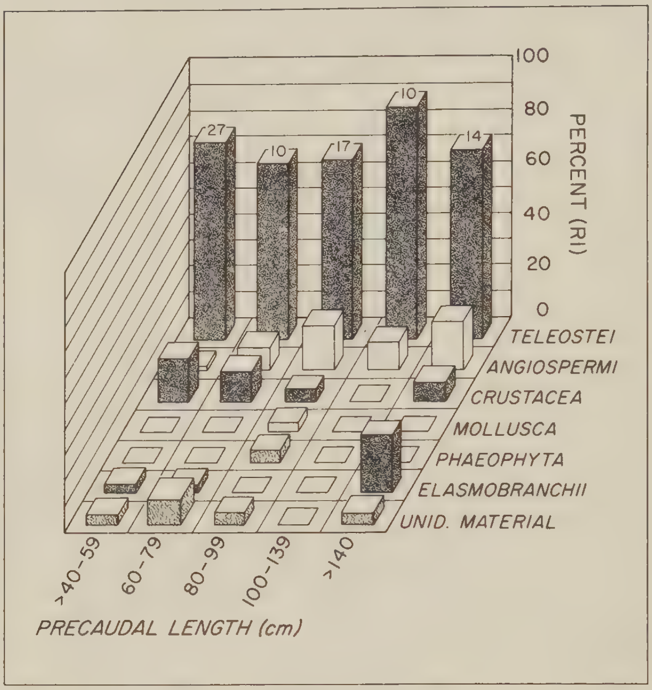

Figure 1.
Variation in the Relative Importance Index (RI) of the major food categories in the diet of five length-classes of lemon sharks off Bimini, Bahamas, and the Florida keys (*N* = 78). Sample size for each length class is given in the figure. (From Cortes and Gruber, In press.)

The opportunistic feeding nature of sharks is suggested by changes in diet with size, season, and habitat. Lemon sharks occupy shallow bays and lagoons during the first few years of life and appear to stray little from these habitats. As they grow, they move off the flats into deeper water, increasing home range, variety of habitats and prey encountered (Gruber 1982; Gruber 1984; Gruber et al. 1988). The diversity of the diet also increases and elasmobranchs, adult jacks, and lobster become increasingly important (Fig. 1). Springer (1960) also noted movement out of nurseries and subsequent changes in the diet of lemon sharks as they increased in size.

Ontogenetic change in diet with increasing size is common in other species of sharks, as is the use of relatively protected environments as nursery areas. The diet of the young leopard shark consists almost exclusively of crabs; older leopard sharks are not restricted to nursery areas and have a much more varied diet, nearly half of which is fish (Talent 1976). Springer (1960) noted that mature sandbar sharks feed on a wide variety of fish, crustaceans, and octopus, while Medved et al. (1985) found that blue crabs and menhaden comprised the majority of the diet of young sandbar sharks caught in an estuary. Juvenile Port Jackson sharks occupying bays and estuaries feed on soft bodied invertebrates, while the main prey of adults is a variety of echinoderms, mollusks, and crustaceans (McLaughlin and O'Gower 1971). Young soupfin sharks, which inhabit bays with subtidal flats, feed largely upon fish, crustaceans, and mollusks; but adults feed around rocky areas and consume more fish and octopus (Olsen 1954). As spiny dogfish grow, their diet becomes more diverse and shifts from invertebrates to fish (Jones and Geen 1977). Larger kitefin sharks consume more crustaceans, teleosts, and elasmobranchs, while the importance of cephalopods in the diet declines with an increase in size (Matallanas 1982). Lyle (1983) found that young lesser spotted dogfish ate more crustaceans, while larger specimens ate more mollusks and fewer crustaceans. Finally, when mako sharks had attained a size greater than 150 kg, they were able to feed on very large prey such as swordfish (Stillwell and Kohler 1982).

These ontogenetic changes in diet indicate that in some species of sharks, juveniles have a restricted diet associated with a particular habitat such as a nursery ground. In these areas young sharks may be less susceptible to predation, but also may encounter fewer potential prey. Particularly abundant prey, or one which is easily caught, may dominate diets of young sharks which live in nursery areas.

Seasonal shifts in the diet of young lemon sharks have not yet been confirmed, but it appears that there may be a peak in consumption of toadfish, *Opsanus beta*, which coincides with increased vocalization during toadfish mating season each April (Cortes 1987). There have been many reports of seasonal changes in the diet of other sharks. As seasonal abundance of different species of squid fluctuates, the amount of each species consumed by blue sharks also fluctuates (Tricas 1979). Talent (1976) found that leopard sharks ate primarily fish during the summer, but primarily crabs and clams during the fall. The importance of bluefish and squid in the diet of the mako shark shifts with season (Stillwell and Kohler 1982). Bluefish are more important during the spring and winter, but migrate inshore during the summer, and are replaced in importance by cephalopods. Matallanas (1982) discovered that while teleosts were the most important prey item in the diet of kitefin sharks throughout the year, the items of secondary importance shifted with season. Sharks were the second most common item in spring and winter, crustaceans in summer, and cephalopods in the fall. When herring were concentrated in large numbers during spawning periods, they became a major prey item in the diet of the lesser spotted dogfish (Lyle 1983). During seasonal migrations, certain fish may become important dietary items for the soupfin shark (Olsen 1954).

Habitat may have a significant influence in the type of prey recovered from the stomachs of sharks. Cortes (1987) found little difference between the diet of lemon sharks sampled off the Florida Keys and Bimini, Bahamas. However, Schmidt (1986) recorded large numbers of shrimp in the stomachs of lemon sharks caught in Florida Bay, while few shrimp were found in stomachs examined by Cortes.

The contribution of fish and crustaceans to the diet of scalloped hammerhead sharks, *Sphyrna lewini*, varied from one location to another in Kaneohe Bay, Hawaii (Clarke 1971). The relative importance of mollusks and demersal fish in the diet of lesser spotted dogfish also varied with sampling location (Lyle 1983). Olsen (1954) noted that the diet of young soupfin sharks was dependent on which estuary the sharks inhabited. Bowman (1986) found that spiny dogfish ate more squid in deep water, but switched to fish in shallow water. The percentage occurrence of prey items in stomachs of mako sharks has also been correlated with location (Stillwell and Kohler 1982). Clarke and Stevens (1974) found different cephalopod species in the stomachs of blue sharks captured at two different locations. Further opportunism is suggested by their feeding on fish in the epipelagic zone, squid in deep water, and crustaceans and gastropods when feeding on the bottom (Stevens 1973). The diet of blue sharks also varies depending on the availability of anchovies, squid, or salmon (Le Brasseur 1964; Tricas 1979). Horn sharks, *Heterodontus francisci*, were reported to abandon nocturnal feeding habits and to feed during the day when large numbers of dead or dying fish were present (Finstad and Nelson 1975). These findings demonstrate that sharks can switch to different prey in different habitats and that food habits in one location may not be representative of food habits of the same species elsewhere. Thus, limited sampling of stomach contents of sharks, both in time and space, must be interpreted with caution.

Tiger and bull sharks provide examples of species which have broad feeding habits. The tiger shark is considered to be an opportunistic feeder, preying on a wide range of organisms (Bell and Nichols 1921; Springer 1960; DeCrosta et al. 1984). Bull sharks select a wide variety of habitats, ranging from freshwater lakes and rivers, to coral reefs and flats throughout the tropical and subtropical oceans (Compagno 1984). Just as habitats selected by the bull shark are extremely diverse, so is the diet. Tuma (1976) found echinoderms, mollusks, crustaceans, mammals, teleosts, elasmobranchs, reptiles, and other items in the stomachs of bull sharks. These sharks were capable of capturing fast swimming fish, but consumed almost any type of animal matter available (dead or alive). Hobson (1963) believed that while sharks may feed on injured, distressed, or dead fish, they were capable of capturing highly motile, elusive prey. Versatile food habits are advantageous to the individual because feeding will not be limited to a particular prey item throughout the year. With sharks, this may allow for an increase in population density, a decrease in competition and a broadening of range and distribution (Talent 1976).

Shifts in prey selection may be due to changes in abundance, ease of capture of prey, or changes in density of shark populations (Talent 1976). It appears that in several species, the most abundant prey items in a habitat are also the most heavily preyed upon. The most prominent prey items in the diet of juvenile lemon sharks appear to be among the most abundant organisms in the shallow water environments inhabited by the sharks; however, further studies directed toward this question are currently underway (Gruber, unpubl. data). Lyle (1983) concluded that the most common prey in the diet of lesser spotted dogfish were also the most abundant species in a survey of bottom fauna. A similar conclusion was reached by Clarke (1971) for the scalloped hammerhead shark and by Talent (1976) for the leopard shark.

Some shark species demonstrate the ability to select prey. Springer (1960) described the sandbar shark as a discriminating bottom feeder, which showed a preference for specific prey. Stillwell and Kohler (1982) suggested that the mako shark may selectively feed on larger bluefish to maximize rate of energy intake. Tricas (1979) observed several patterns of predatory behavior by blue sharks when they fed upon schools of spawning squid. The feeding patterns reported by Tricas varied with size and activity of shark, as well as the physical configuration and alertness of squid. Even the bull shark has shown evidence of selective feeding, passing up abundant species of fish which were regularly consumed by other species of shark (Snelson et al. 1984).

The observation of a preference for specific prey, as well as changes in prey selectivity, introduce the question concerning the degree to which sharks are selective in their feeding habits. The relationship between opportunistic and selective feeding in sharks is not evident to us. Both opportunistic and selective feeding habits can be described for sharks, and even for individuals of the same species. Many sharks may fit the description of opportunistically-selective feeders. When food is abundant, they may select a specific item, which may maximize energy intake with a minimum of energy expenditure. When food is less plentiful, they may not be afforded the luxury of choice, and may feed on almost any prey which is available. In lemon sharks, the interval between meals is relatively long (Cortes 1987). Sharks that eat infrequently may feed when a preferred food item is encountered, rather than consuming less desirable prey more frequently.

Optimal Foraging

The theory of optimal foraging is based on the evolutionary premise that individuals within a population that forage most efficiently and that maximize their net rate of energy intake will possess greater fitness and contribute their genes to future generations (Townsend and Winfield 1985). There are two extremes in feeding habits that maximize foraging efficiency: indiscriminate feeding at low prey abundance, and selective feeding on larger, energy rich items when prey is abundant (Knights 1985). Changes in sensory ability that occur with age may strongly influence feeding strategy. Young fish, growing at a maximum rate, have a large appetite and are generally less selective of prey. They may also lack the sensory capability to distinguish between potential prey items. As visual and chemical cues are learned, older fish may become more selective of larger, higher quality prey (Knights 1985).

There is considerable confusion and disagreement about the usefulness of this theory, but it is possible to briefly view the feeding habits of the lemon shark from this perspective. First we can examine changes in sensory capability of lemon sharks as they age. Although the lemon shark is farsighted, young lemon sharks appear to have better visual acuity than older sharks (Hueter and Gruber 1982). Beulig (1982) found that young lemon sharks did not instinctively recognize the sound of prey, but had to learn specific sounds associated with the availability of food. Thus, as their senses develop and prey abundance increases, young lemon sharks should feed on a more narrow range of prey, increasing their selectivity as they grow. However, Cortes (1987) found that the diet of lemon sharks become more diverse with age. So young lemon sharks may lack the ability to catch a variety of prey or may simply not encounter that variety of prey in the nursery habitat. Similar limitations may apply to other species of shark that inhabit areas of low productivity at early ages. In these cases sharks may not appear to conform to the tenets advanced in the theory of optimal foraging. Casey et al. (1985) suggested that sandbar sharks may reach a size where food, oxygen, or a combination of several factors become limiting and this is the putative mechanism which triggers juveniles to leave nursery areas for offshore waters. As more information is gathered about the life-history strategies of elasmobranchs and about optimal foraging in other taxa, many of the existing principles may be more readily understood.

Finally, there are several reports of sharks feeding cooperatively. Although the lemon shark may congregate loosely in schools (Gruber et al. 1988), there has been no documentation of cooperative hunting in this species. Lineaweaver and Backus (1969) state that the oceanic whitetip shark, *Carcharhinus longimanus*, may hunt cooperatively and Budker (1971) made a similar statement about thresher, *Alopias* sp., and sandtiger sharks, *Eugomphodus taurus*. Randall (1977, 1986) commented on the possibility of cooperative hunting by other species of sharks. Talbot (F.H. Talbot, Director, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, pers. comm., June 1987) and others have observed blacktip reef sharks, *Carcharhinus melanopterus*, hunting in groups and chasing small teleosts out of the water onto the shore. The blacktips then beached themselves and fed upon the stranded fish.

Feeding Patterns

It is not only important to know what sharks eat, but also when and how often they eat. Knowledge of food habits

Table 3.
Percentage of sharks caught that had empty stomachs.

Species	% empty stomachs	Reference
Sharks caught using bait		
Notorhynchus cepedianus	92	Herald and Ripley 1951
Carcharhinus amblyrhynchos	80	McKibben and Nelson 1986
Negaprion brevirostris	80	Gruber 1984
Carcharhinus leucas	58	Tuma 1976
Carcharhinus plumbeus	55	Wass 1973
Carcharhinus galapagensis	54	De Crosta et al. 1984
C. amblyrhynchos	48	De Crosta et al. 1984
Isurus oxyrinchus	40	Stillwell and Kohler 1982
Prionace glauca	39	Stevens 1973
P. glauca	37	Clarke and Stevens 1974
Galeorhinus galeus	26	Olsen 1954
Galeocerdo cuvier	20	De Crosta et al. 1984
P. glauca	6	Tricas 1979
Sharks caught using net or other nonbait methods of capture		
Squalus acanthias	74	Bowman 1986
Triaenodon obesus	59	Randall 1977
S. acanthias	36	Jones and Geen 1977
N. brevirostris	26	Cortes and Gruber In press
Dalatias licha	17	Matallanas 1982
P. glauca	17	Le Brasseur 1964
Triakis semifasciata	16	Talent 1976
C. plumbeus	13	Medved et al. 1985
Scyliorhinus canicula	1	Lyle 1983

is vital in assessing the ecological requirements of a species (Talent 1976), and information gathered on diet and feeding habits adds insight into the biology and distribution of a species (Stillwell and Kohler 1982). Two questions of fundamental importance to understanding the interaction between a predator and food resources are "How often and how much does the predator consume?" (Hall 1987).

The feeding schedule of the lemon shark appears to be characterized by short bouts, followed by longer periods of digestion, with little or no feeding in the interim. This pattern appears to hold for other species as well. For example, individuals are often caught and found to have empty stomachs. Cortes (1987) found that 26% of lemon sharks captured with gill nets had empty stomachs. This is low in comparison to values reported for other species (Table 3). Springer (1960) wrote that a very large proportion of sharks in commercial landings had empty stomachs. This means that a large number of animals caught with bait had gone a substantial period of time without eating. Yet some individuals caught with bait have full stomachs, which reinforces the common perception that sharks are "gluttons" (Budker 1971). Lineaweaver and Backus (1969) reported large catches of sharks with full stomachs, and on other occasions poor catches characterized by a high percentage with empty stomachs.

Many food items in the stomachs of sharks are well digested. In the lemon shark, 28% of stomachs containing food had a single item in a late stage of digestion (Cortes 1987). The same was true for 21.5% of sandbar sharks that had food in their stomachs (Medved et al. 1985). Thus, nearly 50% of lemon and sandbar sharks had little or no food in their stomachs when captured. Springer (1960) noted that stomach contents of sandbar sharks were usually not identifiable owing to an advanced state of digestion. A high frequency of unidentified prey in late stages of digestion is characteristic of the kitefin (Matallanas 1982) and soupfin sharks (Olsen 1954). Stevens (1973) was able to identify only 50% of prey in the stomachs of blue sharks, because most items were in an advanced state of digestion. It is apparent that the majority of sharks that were attracted to bait were those which had relatively empty stomachs or those which had recently eaten, but were still inclined to consume additional food. Thus, these sharks feed for short periods of time.

The number of food items in the stomachs of lemon sharks caught in nets was low. Nearly 80% of stomachs containing food had only one or two prey items (Cortes 1987). Medved et al. (1985) reported a similar finding for the sandbar shark, where 60% of stomachs with food contained a single item and 90% had three items or less. Most blue shark and spiny dogfish stomachs also contained only one or two food items (Stevens 1973; Jones and Geen 1977). Tricas (1979) found a low average number of prey in the stomachs of blue sharks during most of the year.

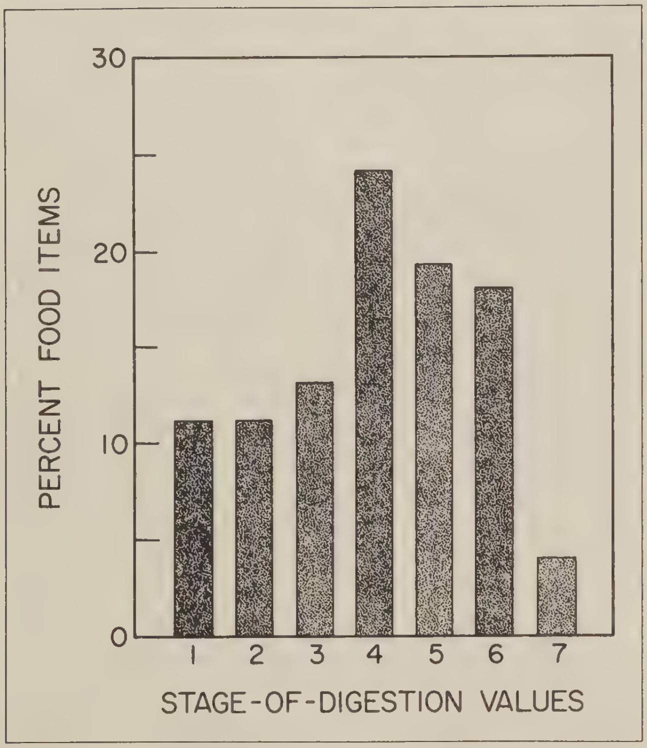

Figure 2.
Frequency distribution of stage-of-digestion values assigned to food items ($N = 110$) consumed by young lemon sharks captured off the Florida keys. (From Cortes 1987.)

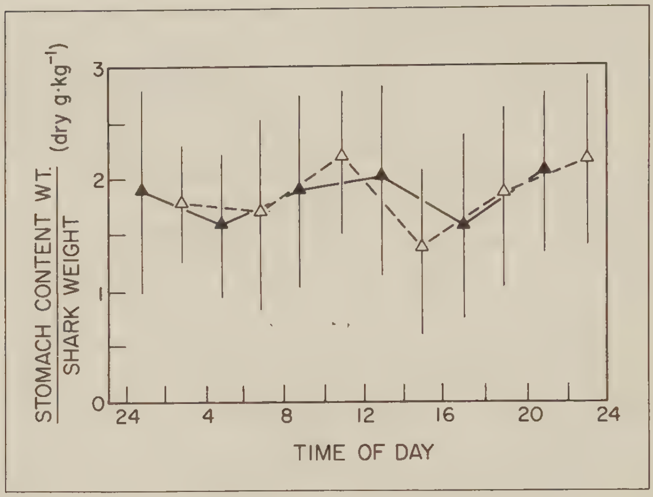

Figure 3.
Diel variation in mean ratio of dry weight of stomach contents to wet weight of shark (g/kg). Solid triangles are the means at the mid-point of each 4 h time interval, starting at 2300 hours; open triangles are the means at the mid-point of each 4 h time interval, starting at 0100 hours. Vertical lines designate ± 1 SD. (From Cortes 1987.)

The average number of food items in the stomachs of lesser spotted dogfish was between four and six (Lyle 1983). In each of these studies, multiple food items were usually in a similar stage of digestion. Cortes (1987) and Medved et al. (1985) assigned stage-of-digestion values, based on rates of digestion in control studies, to food items found in stomachs of lemon and sandbar sharks respectively. Examination of the values for multiple food items allowed them to calculate feeding duration for these two species. Feeding duration of the lemon shark was estimated as 10–11 hours and at 7–9 hours for the sandbar shark. Feeding frequency of the lemon shark was estimated as 32 hours. Thus, an average lemon shark would actively feed for 10–11 hours and then fast for the next 32 hours. Theoretically, if these sharks had been feeding continuously, multiple food items at various stages of digestion would be found in their stomachs. Yet the opposite trend was observed.

Our findings indicate that frequency of feeding in the lemon shark is dependent on factors which commonly influence rate of consumption in other aquatic vertebrates, such as rate of digestion and energy content of food, rather than their ability, or inability to capture prey. After a lemon shark has consumed a meal or successive meals, feeding appears to be reduced. Sharks very likely encounter prey during this time, but they may not be attracted to a potential meal because their stomachs are relatively full. When the stomach is nearly empty, feeding activity increases, and prey may once again be actively sought.

Finally, a cyclical feeding pattern has been described for the captive lemon shark. Peak consumption is followed by a few days of reduced consumption, when appetite is reestablished (Graeber 1974; Longval et al. 1982). Casey et al. (1985) noted a similar pattern for captive sandbar sharks. All of these observations point to a short period of active feeding, followed by a longer period of digestion with reduced feeding activity. There is little evidence to support the supposition that sharks feed continuously, and abundant evidence that feeding motivation waxes and wanes as in most other vertebrates.

Cortes (1987) found food in all stages of digestion in the stomachs of lemon sharks sampled at hourly intervals (Fig. 2). This suggested that lemon sharks feed asynchronously, i.e., there is no particular time of day or night when a greater number of sharks are feeding. Data from Medved et al. (1985) and Matallanas (1982) supported these findings for other shark species.

There is a widespread belief that sharks are more active at night and feeding activity increases during this time (McKenzie and Tibbo 1964). Both laboratory (Nelson and Johnson 1970; Casterlin and Reynolds 1979; Nixon and Gruber 1988) and field studies (McLaughlin and O'Gower 1971; Finstad and Nelson 1975) have shown that metabolic rate or activity of some sharks, including the lemon shark, increases at night. Yet Cortes (1987) found no temporal difference in the amount of food in stomachs of lemon sharks (Fig. 3). Medved et al. (1985) also found no significant day-night differences in stomach contents of sandbar sharks. Actual increase in feeding activity by the lemon and sandbar sharks may be masked by crepuscular feeding habits, or by occasional opportunistic feeding throughout the day or night. Olsen (1954) reported that tides may be a factor in the feeding activity of soupfin sharks, but tidal cycle did not influence feeding of sandbar or lemon sharks (Medved et al. 1985; Cortes 1987). It appears then, for at least the lemon and sandbar sharks, and presumably others, feeding is intermittent, asynchronous, and does not exhibit measurable patterns of periodicity.

Digestion

The digestive abilities of sharks are confusing and difficult to characterize. Sharks may cease feeding for long periods of time for no apparent reason, presumably relying on energy stores in the liver during weeks and even months of starvation (Lineaweaver and Backus 1969; Budker 1971; D.R. Nelson, Department of Biology, California State University, Long Beach, CA 90840, pers. comm., June 1987). Springer (1960) felt that larger prey species were frequently of a less digestible type, and were taken by sharks in desperation when no other food was available. He also hypothesized that the digestive processes of sharks were inhibited when they swallowed large quantities of decomposing flesh of sharks and rays. The acidity of a stomach would decrease due to

> . . . the continuous liberation of ammonia through the action of enzymes produced during the course of ordinary putricative decomposition of the urea that normally occurs in sharks.

Springer (1960) reported that stomachs of sharks which contained large amounts of decomposing shark flesh had a pH above 8.0, whereas those containing fish, turtles, birds, or small amounts of shark flesh had a pH of 4.0 or below.

Budker (1971) reported that the stomach of a shark may retain food in a undigested state for long periods of time. He describes an account of two dolphin fish, *Coryphaena hippurus*, in a perfect state of preservation being recovered from the stomach of a tiger shark that was held in captivity for a month. The shark appeared to have preserved the dolphin, while ingesting and regurgitating horsemeat. This was presumably accomplished by restriction of digestive secretions, compartmentalization, or secretion of preservative substances. Budker (1971) also reported that human flesh had remained undigested in the stomach of a tiger shark for days and even weeks.

The means by which sharks achieve these unusual feats is not clear. Digestive enzymes which are produced in the alimentary tracts of elasmobranchs are substances common to teleosts and other vertebrates (Fange and Grove 1979). Dobreff (in Barrington 1957) found that HCl production continued in the stomach of elasmobranchs deprived of food for 112 days. Acidity declined with the absence of food, but HCl was still secreted in detectable quantities until the animal died of starvation. Observation of feeding behavior in captive sharks, such as prolonged unwillingness to feed, or preservation of food, does not necessarily represent natural feeding or digestive characteristics. Stress associated with captivity can lead to refusal of food and unusual feeding behavior (Van de Elst et al. 1983). Studies of the digestive physiology of elasmobranchs are needed to explain these unusual phenomena.

Most absorption of nutrients takes place in the intestine, and this is an early step in making useful energy available for growth or metabolism (Fange and Grove 1979). The rate of the passage of food through the digestive tract can have important ramifications in the amount of nutrient absorbed across the gut wall. The longer a meal is in the digestive tract, the longer it is subject to the processes of enzymatic digestion and absorption, and the greater the amount of nutrient that can be absorbed (Windell 1978).

Total retention time of a meal has been measured in the lemon shark by an x-radiographic technique, where barium sulfate was incorporated into food (Wetherbee et al. 1987). A minimum of 68–82 hours was required for a meal to be entirely eliminated from the digestive tract of the lemon shark (Fig. 4). Budker (1971) reports that a period of 2–6 days is a typical residence time of a meal in the digestive tracts of sharks, and gives a value of 18 days as the time food remained in the digestive tract of dogfish. It is apparent that food passes through the alimentary tract of sharks at a relatively slow rate compared to most teleosts. For example, the average time for a meal to be completely emptied from the digestive tract of teleosts studied at 20–25°C is less than 50 hours (Lane and Jackson 1969; Fange and Grove 1979).

Differences in digestive processes between elasmobranchs and teleosts are not limited to the rate at which food passes through the gastrointestinal tract. Most teleosts have a tubular intestine, while elasmobranchs have a spiral valve intestine, which increases surface area for absorption without taking up additional space in the body cavity (Budker 1971). This space conservation measure may be correlated with the large elasmobranch liver required for buoyancy, or with retention of developing embryos in uteri (Moss 1984). The digestive and absorptive capabilities of elasmobranchs had not been studied prior to Wetherbee (1988). He found that the lemon shark is able to absorb energy from a meal with an efficiency comparable to that of most teleosts. Absorption efficiency of lemon sharks is not unusually high or low, despite their having a spiral valve intestine, a prolonged food retention time and an extended period of digestion.

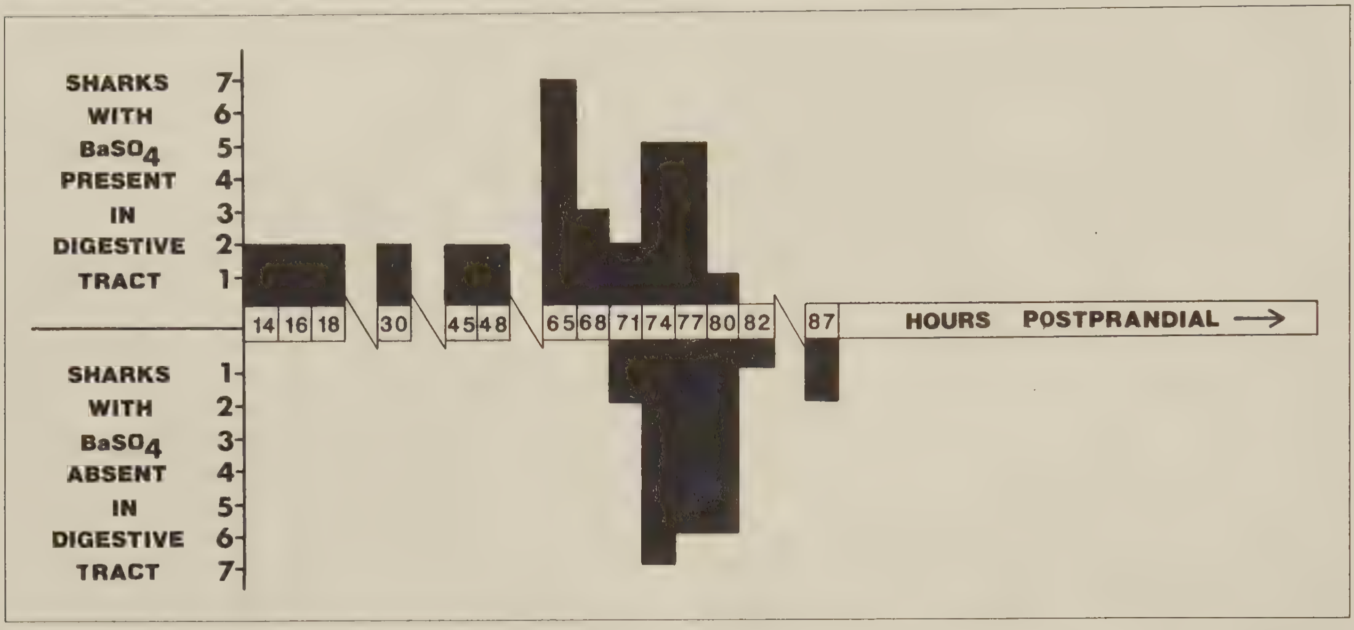

Figure 4.
Histogram showing the presence or absence of barium sulfate ($BaSO_4$) in the digestive tract of lemon sharks. The first observation in which $BaSO_4$ had been completely voided was at 71 hours, while the last occurrence of $BaSO_4$ was at 80 hours.

Consumption

The rate at which food energy passes through an individual, sets a limit on the rate of production for an individual or population (Hall 1987). Food consumed by sharks represents the sole energy source for growth and metabolism, and estimates of consumption can be valuable in assessing basic biological information, ecological relationships, the extent of predation and competition, environmental conditions for growth, impact on commercially important fish or other stocks, and rational exploitation of populations.

Two basic methods have been used to estimate consumption for fishes. One method uses laboratory experiments to derive parameters relating to growth, metabolism, excretion and digestion. The second method estimates consumption based on the amount of food found in stomachs sampled in the wild, in conjunction with measurement of the rate of gastric evacuation (Windell 1978). Both methods rely on experiments with captive animals, and for this reason, there have been very few estimates of consumption for elasmobranchs. The difficulty of keeping and sampling sharks in captivity has limited laboratory studies of many aspects of elasmobranch biology (Gruber and Myrberg 1977; Martini 1978; Gruber and Keyes 1981). Consumption cannot be estimated by using description of prey items, weight, or volume alone. This is because the amount of food found in a stomach is a function of the rate of gastric evacuation, amount of food initially consumed, and time (Windell 1978).

Gastric Evacuation

Two estimates of the time required for complete evacuation of food from the stomachs of lemon sharks have been derived. Schurdak and Gruber (1988) found that filets of blue runner, *Caranx chrysos*, were completely evacuated in approximately 24 hours, and the pattern of gastric emptying was exponential. Cortes (1987) found that a larger meal of a natural prey item was completely eliminated from stomachs in 28–41 hours, and was best described by a linear model. The difference in these two studies may be due to the use of smaller more friable food by Schurdak and Gruber, as well as temperature fluctuation in Cortes' study. Jobling (1986) reviews the influence of these factors on gastric evacuation and the mathematical models that are used to describe the rate of gastric evacuation in fish. He concludes that smaller more easily digested food is rapidly eliminated from stomachs in an exponential manner, while larger items are evacuated in a linear manner.

Medved (1985) showed that time required for complete gastric evacuation in the sandbar shark was 71–92 hours, much longer than that of the lemon shark (Table 4). The difference in time is greater than what might be expected based on their similar distribution, life history, and close phylogenetic relationship. It is likely that methodological differences exaggerated actual differences in gastric evacuation. Medved (1985) force fed sandbar sharks and used a stomach lavage technique to remove stomach contents. Force-feeding in teleosts has been shown to depress the rate of gastric evacuation and increase variation between

Table 4.
Estimates of time required for a meal to be completely evacuated from the stomachs of sharks.

Species	Hours for complete gastric evacuation	Temperature °C	Reference
Squalus acanthias	124	10	Jones and Geen 1977
Carcharhinus plumbeus	71-92	25	Medved 1985
C. plumbeus	48 +	—	Wass 1973
Isurus oxyrinchus	36-48	—	Stillwell and Kohler 1982
Negaprion brevirostris	28-41	20-29	Cortes 1987
N. brevirostris	24	25	Schurdak and Gruber 1988
Prionace glauca	24 +	—	Tricas 1979

individuals (Windell 1966; Swenson and Smith 1973). In the Medved study, stomachs were lavaged prior to a feeding trial; this treatment may have washed digestive enzymes from stomachs, delaying the onset of digestion and perhaps prolonging gastric emptying time. Cortes (1987) estimated time for complete evacuation of lemon shark stomachs by extrapolation from a gastric evacuation curve (Fig. 5). However, MacDonald et al. (1982) found that rate of gastric evacuation may peak after a time, so that a linear representation of evacuation rate, similar to Cortes' may be improper. Lemon sharks were also held at a slightly higher temperature than sandbar sharks. Temperature has been shown to hasten gastric emptying in teleosts (Jobling 1986). Considering the different techniques used by Medved and Cortes, it is likely that the actual times required for complete gastric emptying in the lemon and sandbar sharks are more similar than would appear from the results.

Other estimates of gastric evacuation rates for sharks are not well documented or are incomplete. Jones and Geen (1977) force fed spiny dogfish extremely high rations and estimated time for complete gastric emptying by fitting a straight line to the data and extrapolating to zero food. Stillwell and Kohler (1982) estimated time for complete gastric emptying for the mako shark based on examination of stomach contents and use of information from other species of sharks. Rate of gastric evacuation and time required for complete emptying were not actually measured in either of these studies. Wass (1973) found that sandbar sharks had food in their stomachs 48 hours after consumption of a meal but did not determine time for complete gastric evacuation. Tricas (1979) reported the presence of undigested food in stomachs of blue sharks 24 hours after consumption of a meal. Based on the few actual measurements and partial measurements of gastric evacuation, it is apparent that a substantially longer period of time is required for food to be completely eliminated from the stomachs of sharks than the stomachs of teleosts. Although gastric evacuation of several teleosts may require over 30 hours, the average time for complete gastric evacuation of a meal measured for teleosts at a temperature close to 25°C is about 12 hours (Fange and Grove 1979).

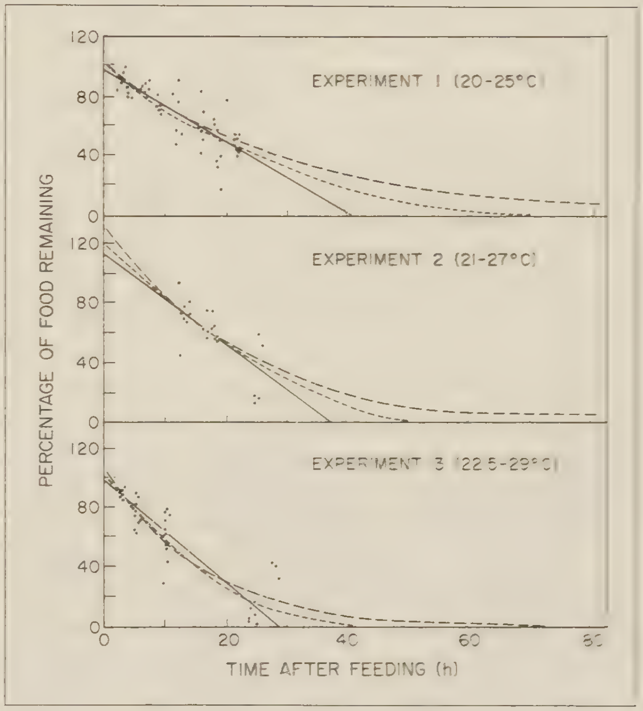

Figure 5.
Mathematical models fitted to gastric evacuation data of young lemon sharks fed snapper or white grunt, at three temperature regimes: linear (——), exponential (— — —), and square root (- - - -). Percentage of food remaining in stomachs is expressed as dry weight. (From Cortes 1987.)

Daily Ration

Although an individual may not consume the same amount of food each day, or may not even feed daily, consumption expressed on a daily basis (daily ration) provides a useful means of comparison of ingestion rates for different

Table 5.
Estimates of daily ration for sharks.

Species	Daily ration % body weight/day	Reference
Isurus oxyrinchus	3.2	Stillwell and Kohler 1982
Negaprion brevirostris	1.5–2.1	Cortes 1987
Squalus acanthias	1.3	Jones and Geen 1977
Carcharhinus plumbeus	1.1	Medved et al. 1988
N. brevirostris	0.4–2.0	Clark 1963
S. acanthias	0.4	Brett and Blackburn 1978

Table 6.
Estimates of annual consumption for sharks.

Species	Daily ration % bw/d	Average body weight (kg)	Annual consumption (kg)	Body weight[a] consumed	Reference
Isurus oxyrinchus	3.1	69.0	781	11.3	Stillwell and Kohler 1982
Negaprion brevirostris	1.5–2.1	1.891	10.3–13.8	5.8–7.3	Cortes 1987
N. brevirostris	—	1.000	5.3–6.5	5.3–6.5	Bushnell et al. submitted
Squalus acanthias	1.3	0.107	0.51	4.7	Jones and Geen 1977
Carcharhinus plumbeus	1.1	1.882	7.6	4.0	Medved et al. 1988
S. acanthias	0.4	0.107	0.16	1.5	Brett and Blackburn 1978

[a] Body weight consumed = number of times an equivalent of body weight is consumed in a year.

organisms. Daily ration of the lemon shark has been estimated at about 2% body weight per day (bw/d) (Cortes and Gruber, In press). Clark (1963) stated that lemon sharks held in captivity consumed between 0.4 and 2% bw/d and assumed that daily ration in the field was higher than in captivity because of the need for additional energy to capture prey. Gruber and Stout (1983) showed that captive lemon sharks kept under optimal conditions grew ten times faster than in the wild. The majority of additional growth observed by Gruber and Stout can be attributed to food intake levels, which were about 3% bw/d and well above those of wild lemon sharks. Changes in metabolic rate and stress would also influence growth rate in captivity sharks.

Table 5 lists estimates of daily ration for other species of sharks. Medved et al. (1988) obtained a value of 1.1% bw/d for daily ration of sandbar sharks. The lemon shark appears to consume almost twice as much food as the sandbar shark, but differing estimates of gastric evacuation rate may be partly responsible for different estimates of consumption. Another factor may be that lemon sharks grow more rapidly and to a greater size than sandbar sharks (Casey et al. 1985; Henningsen and Gruber, in prep.). If lemon sharks have a higher metabolic rate than sandbar sharks, they would require an increased level of intake for metabolism, yet reports of activity of these two species are somewhat conflicting (Medved and Marshall 1983; Nixon and Gruber 1988).

Daily ration of the spiny dogfish has been calculated to be 1.3% bw/d (Jones and Geen 1977) and 0.4% bw/d (Brett and Blackburn 1978), the difference attributable to methodology. Bowman (1986) cautioned that spiny dogfish caught at depth frequently regurgitate stomach contents when they are brought to the surface. This would result in a bias in determination of daily ration and the type of prey consumed; and the predatory impact that spiny dogfish have on fish populations would be underestimated.

Stillwell and Kohler (1982) estimated daily ration of the mako shark at 3.1% bw/d. Although this estimate was not based on measurement of the rate of gastric evacuation, a high level of consumption relative to other shark species might be expected. Mako sharks are fast swimming, highly active sharks, capable of maintaining a body temperature several degrees above that of ambient water (Carey and Teal 1969). Digestion rate, rate of food passage, and consequent ingestion rate may all be increased at higher ambient temperatures (Jobling and Davies 1979; Kaushik 1986). This may be especially true considering that the spiral valve is the warmest visceral organ in the mako shark (Carey et al. 1981). Mako sharks grow at a fairly rapid rate in comparison to many sharks (Pratt and Casey 1983). This also implies a high level of intake, assuming that assimilation and growth efficiencies are similar to those of cold bodied sharks.

Table 7.
Estimates of annual growth in mass for individual sharks of the species listed.

Species	Initial weight (kg)	Final weight (kg)	Weight gain (kg)	% body gain	Reference
Negaprion brevirostris	1.118	2.664	1.546	138	Henningsen and Gruber, in prep.
Carcharhinus plumbeus	1.349	2.415	1.066	79	Medved et al. 1988
Squalus acanthias	0.092	0.122	0.031	33	Jones and Geen 1977

Table 8.
K values = slope of von Bertalanffy growth curve fitted to growth data for sharks.

Species	*K* value	Reference
Rhizoprionodon terraenovae	0.35–0.50	Branstetter 1987
Carcharhinus limbatus	0.27	Branstetter 1987
Isurus oxyrinchus	0.20–0.27	Pratt and Casey 1983
Prionace glauca	0.22	Branstetter 1987
Carcharhinus brevipinna	0.21	Branstetter 1987
Galeorhinus galeus	0.16	Olsen 1984
Carcharhinus leucas	0.08	Branstetter and Stiles 1987
Squalus acanthias	0.05–0.07	Ketchen 1975
Negaprion brevirostris	0.06	Brown and Gruber 1988
Carcharhinus plumbeus	0.04–0.05	Casey et al. 1985

Despite problems encountered in determining consumption rate, it is apparent that sharks consume less on a percentage body weight basis than most teleosts. Many carnivorous teleosts consume 20–30% bw/d (Brett and Groves 1979), while the maximum ration voluntarily consumed by lemon sharks (growing ten times faster than wild sharks) is less than 3% bw/d (Gruber 1984).

Based on average body weights and estimates of daily ration, annual rate of consumption can be calculated for the lemon shark and several other species. When annual consumption is expressed as the number of times an equivalent of body weight is consumed, comparisons between sharks of different sizes are possible (Table 6). Also included in Table 6 are several estimates of annual consumption based on the energetic requirements for metabolism. The high level of annual consumption by mako sharks is consistent with greater energy requirements of this species, whereas the level of consumption by spiny dogfish, a cold water species with a low metabolic rate, is low (Brett and Blackburn 1978).

Production

Based on annual growth rates, annual production can be estimated for young sharks of several species. Again, for ease of comparison of species of different sizes, annual production for an individual is expressed as percentage increase of initial body weight (Table 7). Rates of production of most teleosts, based on annual increases in body weight, are higher than that for elasmobranchs listed in Table 7. Many teleosts double their body weight in less than a week, which represents a tremendous weight increase on an annual basis (Brett and Groves 1979).

Other sharks appear to grow at faster rates than those shown in Table 7. Branstetter (1987, 1990) proposed that growth rates of sharks are correlated with the ecology of each species. Growth rates of sharks (lemon, bull, sandbar) that inhabit shallow bays and estuaries early in life are relatively slow. Other species such as Atlantic sharpnose, *Rhizoprionodon terraenovae*; spinner, *Carcharhinus brevipinna*; blacktip, *Carcharhinus limbatus*; and blue shark, have relatively rapid growth rates (Table 8). In these species, parturition occurs in offshore waters, making pups more susceptible to predation, thus favoring rapid growth in these environments. These life history traits may represent two different strategies for improving the survival rate of young. Although consumption has not been measured for fast-growing species, higher levels of growth may be dependent on increased levels of consumption.

Gross conversion efficiency (K_1) represents the efficiency of food conversion to growth (Brafield and Llewellyn 1982). Using values obtained for daily ration and growth, we have calculated conversion efficiencies for several species of sharks on an annual basis (Table 9).

Table 9.
Estimates of gross conversion efficiency (K_1), the efficiency of food conversion to growth, for sharks on an annual basis.

Species	Annual production (kg)	Annual consumption (kg)	K_1	Reference
Carcharhinus plumbeus	1.066	7.56	14.1	Medved et al. 1988
Negaprion brevirostris	1.546	10.35–13.80	11.2–14.9	Cortes 1987
Squalus acanthias	0.031	0.51	5.9	Jones and Geen 1977

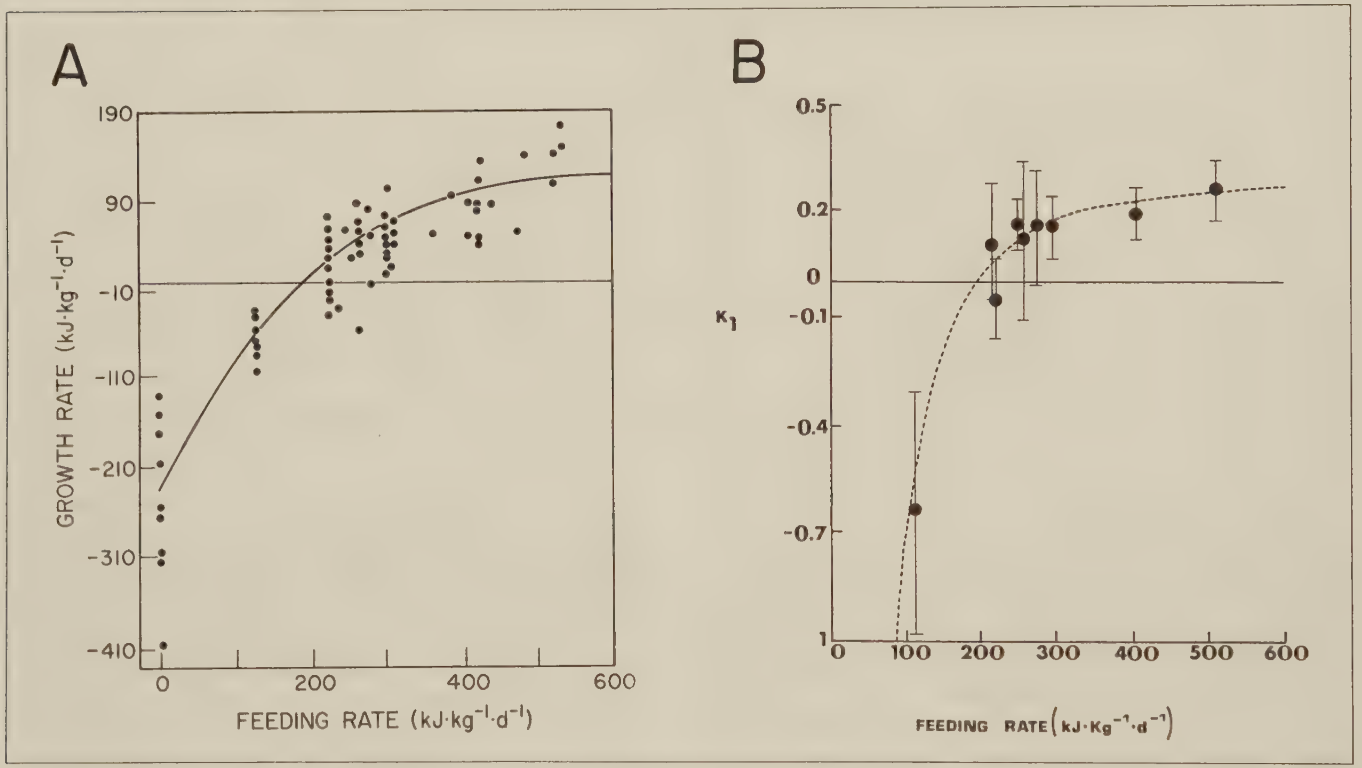

Figure 6.
A. Growth rates for young lemon sharks at 25°C as a function of feeding rate. (From Cortes 1987.) B. Gross conversion efficiencies for young lemon sharks at 25°C as a function of feeding rate. Circles are experimental means, vertical bars designate ± 1 SD. The best fitting curve was traced by eye. (From Cortes 1987.)

The considerable economic and biological importance of fish are incentives for attempting to understand more completely their rates of production (Gerking 1954). Since food supply is the major factor controlling production of most animals, understanding the relationship between food supply and growth is a necessity. Cortes (1987) conducted a series of experiments aimed at establishing the relation between feeding level and production in the juvenile lemon shark. Growth associated with various levels of energy intake were recorded and represented in terms of rate and efficiency (Figure 6, A and B). Cortes found that increasing intake and growth were directly correlated, but growth rate leveled off at high rations.

According to Brett et al. (1969), measurement of food conversion efficiency may well offer one of the greatest sources of insight concerning what governs the success of an animal. We have determined food conversion efficiency of lemon sharks, and found that it continues to increase with increased ration, eventually leveling off at high rations. At intake levels above maintenance, K_1 of the lemon shark is between 10 and 25, which is comparable to values reported for teleosts (Brett and Groves 1979). At the maximum ration voluntarily consumed, Cortes found growth rate and K_1 continued to increase. In several studies involving teleosts, K_1 peaks at an optimum feeding rate and decreases at intake levels beyond the optimum

(Paloheimo and Dickie 1966; Huisman 1976; Elliott 1982; Borgmann and Ralph 1985). Food is not converted to growth as efficiently at these high ration levels owing to factors such as increased activity, decreased absorption efficiency or increased metabolic costs of processing the additional food (Warren and Davis 1967). However, we were unable to induce young lemon sharks to voluntarily feed at intake levels high enough to yield lower growth efficiencies.

Laboratory measurements of growth and conversion efficiency for the lemon shark compare well with information obtained from the field. We were able to estimate the level of consumption required to support rate of field growth, as determined from tag and recapture data, from the growth curve for captive lemon sharks (Figure 6A). Daily ration in the field was estimated to be 1.5 to 2.0% bw/d, which corresponded well with estimates of daily ration obtained by analysis of stomach contents and rate of gastric evacuation (Table 4). Using the laboratory derived K_1 curve in Figure 6B, the K_1 expected for lemon sharks feeding at a rate comparable to the daily ration level was calculated. The generated values of 10–12 agree well with K_1 (11.2–14.9) calculated on an annual basis from field estimates of growth and consumption (Table 9). Thus, estimates of consumption and production in both the laboratory and the field are in agreement.

Growth does not appear to be limited by the ability of the lemon shark to absorb energy, or to convert consumed energy to growth. Experiments conducted by Bushnell (1982) showed that the lemon shark has a metabolic rate comparable to active teleost predators, indicating that metabolic costs were not unusually high. The major factor responsible for slow rates of growth observed in lemon sharks (Gruber and Stout 1983; Henningsen and Gruber, in prep.) is a relatively low level of consumption, which may in turn be limited by a slow rate of digestion.

Applying values of individual consumption and production to a population of lemon sharks in the field may be valuable in assessing the impact of this species on a local level. The population of juvenile lemon sharks inhabiting the north lagoon of Bimini, Bahamas has been estimated at approximately 87 individuals (Henningsen and Gruber, in prep.). An ecosystems modelling study has shown that this ecosystem can support about 250 juvenile lemon sharks (Jacobsen 1987). If these estimates are realistic, then competition between young lemon sharks may not be extreme in this habitat, and food may not be limiting. On the other hand, teleost and elasmobranch predators may compete heavily for food with the lemon sharks, and this competition may lead in turn to intense intraspecific competition.

Conclusions

The lemon shark is a member of the most speciose family of sharks (Carcharhinidae), and conclusions drawn about many aspects of feeding, digestion, consumption, and production in this species may be applicable to many other species of sharks. Considering the number of species of sharks, and the variety of habitats occupied by different individuals, populations, and species, few generalizations are likely to hold for all sharks under all circumstances. Given the extreme variation in food types and prevailing environmental conditions which are selected by sharks, exceptions to generalizations are even more likely. As the number of species under investigation grows, and our understanding of the ecology of these animals improves, previous conclusions will be abandoned and new theories will be accepted. There are, however, several generalizations with respect to feeding ecology that may be appropriate: 1) Sharks are generally opportunistic feeders, able to use a variety of prey in a variety of habitats throughout the year; 2) Sharks may feed most heavily upon the most abundant prey item, opportunism and selectivity being modified by the availability of prey; 3) Feeding occurs in short bouts, followed by longer periods of digestion, when feeding is reduced; 4) Feeding is asynchronous and feeding periodicity has not been well established; 5) Time for complete gastric evacuation and for elimination of a meal from the digestive tracts of sharks is substantially longer than those of most teleosts; 6) Estimates of daily ration for sharks are lower than those for most teleosts; 7) Relative annual consumption and production is lower for sharks than for most teleosts; 8) The lemon shark (and presumably other species) is capable of absorbing and converting energy to growth with efficiencies comparable to those of teleosts.

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A Review of Selected Physiological Characteristics Unique to Elasmobranchs

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ABSTRACT

Elasmobranchs and holocephalians possess several unique physiological characteristics. Four characteristics are discussed in this review: 1) A fatty liver and high hepatosomatic index present in all elasmobranchs examined; 2) A salt-excreting rectal gland which undergoes regression when sharks and rays live in fresh water; 3) An interrenal gland which secretes a steroid hormone and which is present as one or more compact masses between the kidneys separate from the chromaffin tissue (the secreted corticosteroid 1α-hydroxycorticosterone is unique to elasmobranchs); 4) A high plasma concentration of urea (2,000–2,500 mg/100 mL). Elasmobranchs are ureosmotic animals. In the elasmobranch kidney, almost all urea (90–95%) filtered from the renal glomerulus is reabsorbed in the renal tubules.

Introduction

In this brief review, I describe four physiological characteristics which are unique to the elasmobranchs. These include: 1) the fatty liver; 2) the rectal gland, a salt-excretory organ; 3) the interrenal gland and its secretion; and 4) the kidney structure as it relates to ureosmotic vertebrates.

The Fatty Liver

Chondrichthyans have large fatty livers (Corner et al. 1969; Løvtrup 1977). Histologically, these livers more resemble a mass of adipose cells than glandular tissue (Burger 1967; Oguri 1978a). As a result, the hepatosomatic index (HSI), expressed as a percentage ratio of liver weight to body weight is usually high in cartilaginous fishes (Table 1; and Baldridge 1970). For example, the HSI in four species of sharks collected from the eastern Gulf of Mexico by Baldridge (1970) was 10.15% for the bull shark, *Carcharhinus leucas*, 12.41% for the sandbar shark, *C. milberti*; 9.08% for the lemon shark, *Negaprion brevirostris*; and 10.42% for the tiger shark, *Galeocerdo cuvieri*. I calculated these values using Baldridge's data. HSI was also determined for five other species of Chondrichthyans (Oguri 1978a, 1978b, 1985) and was found to be variable according to species (Table 1). Histological examination, however, reveals fatty livers in all species investigated. For example, in one specimen of the South American freshwater stingray, *Potamotrygon* species, the HSI is only 2.94%. Yet, this liver is fatty and contains an abundance of fat droplets stainable with Oil Red O (Oguri 1985).

Hydrocarbons, such as squalene, are a predominant component of lipids stored in the fatty liver, especially in deep sea chondrichthyans (Heller et al. 1957; Blumer 1967; Corner et al. 1969; Gunstone et al. 1986). These stored lipids have very low specific gravities (squalene, 861 kg m^{-3}; Bone and Marshall 1982). Therefore, these low density materials may be used as sources of static lift (buoyancy control) in Chondrichthyes which lack swim bladders (Bone and Roberts 1969). In addition, the fatty liver may act as a lipid nutrient reservoir for the adult fishes and developing embryos (Bone and Roberts 1969).

The Rectal Gland: A Salt Excretory Organ

Sodium concentration in the blood plasma of marine elasmobranchs is lower than that of seawater, but higher than that in the plasma of marine teleosts. For example, the sodium concentration of seawater, the blood plasma of the leopard shark, *Triakis scyllia*, and the saltwater eel, *Anguilla japonica*, are 482, 231, and 153 mM/L, respectively (Hirano 1978). To maintain plasma sodium levels lower than

Table 1.
Hepatosomatic indexes of some cartilaginous fishes
(Oguri 1978a, 1978b, 1985).

Species	Number of fish	Body weight (g)	Hepatosomatic index (%)
Scyliorhinus canicula	10	512 ± 55*	6.06 ± 0.54*
Urolophus aurantiacus	8	355 ± 29	4.60 ± 0.30[a]
Potamotrygon spp.	6	124 ± 14	3.17 ± 0.27
Chimaera monstrosa	13	1159 ± 73	16.01 ± 0.41
Hydrolagus colliei	14	883 ± 90	16.96 ± 0.66

*Mean ± S.E.
[a]unpublished data.

seawater, these fishes must excrete salt. In marine bony fishes, the gills carry out this function (Kirschner 1980). In the marine chondrichthyans, the rectal gland excretes salt (Burger and Hess 1960; Burger 1962, 1965; Hayslett et al. 1974; Kirschner 1980). In the gills of bony fishes, so-called "chloride cells" are the site of sodium excretion (Foskett and Scheffey 1982). Rectal glands and the chloride cells of the gills are often termed "salt glands." The presence of chloride cells in the elasmobranch gills has been reported in the small-spotted catshark, *Scyliorhinus canicula*, and the thornback ray, *Raja clavata* (Wright 1973; Laurent and Dunel 1980). However, salt excretion from elasmobranch gills is not fully understood (Evans 1980).

Several other diverse groups of marine vertebrates also possess salt glands. The nasal gland of marine birds, the lachrymal gland in marine iguana and turtles, and the posterior sublingual gland in sea snakes are examples (Bonting et al. 1964; Hughes 1970; Schmidt-Nielsen and Fänge 1958; Dunson 1969; Peaker and Linzell 1975). Respective salt gland weights of marine birds vary from 87 to 105 mg per 100 g of body weight (Bonting et al. 1964; Hughes 1970). The values in marine reptiles range from 43 to 61 mg per 100 g of body weight (Schmidt-Nielsen and Fänge 1958; Dunson 1969; Peaker and Linzell 1975). In contrast, the weights of elasmobranch rectal glands are low, ranging from 6.7–27.3 mg per 100 g of body weight (Oguri 1981, and Table 2).

Histologically, the rectal gland of elasmobranchs is a compound tubular gland. Its cytological structure in marine dwelling elasmobranchs suggests active salt excretion, because the tubular cells are large and their cytoplasm granules can be stained with acid dyes such as eosin and phloxine (Oguri 1964). In comparative studies of the salt-excreting function of the rectal gland, freshwater elasmobranchs are useful research animals because they live in an environment of very low salt content. Examples include the bull shark *Carcharhinus leucas* of Lake Nicaragua and South American stingrays, *Potamotrygon* spp. The rectal gland of bull sharks collected in Lake Nicaragua and Rio San Juan (which connects the lake to the Caribbean Sea) reveals regressive changes suggesting that the activity of the gland decreases when the animal enters freshwater (Oguri 1964; Gerzeli et al. 1969). Furthermore, Thorson et al. in 1978 reported that the rectal gland of the South American freshwater stingrays, *P.* spp., is in a degenerative state. Mizue and Otake (1983) confirmed this observation. Similar histological results were obtained using *P.* spp. (Oguri, unpubl. data). Since the rectal gland functions to eliminate excess sodium and chloride from the elasmobranch body tissues in seawater, it is conceivable that salt excretion would stop and atrophy if the rectal gland occurred in freshwater stingrays living exclusively in freshwater.

The Interrenal Gland and 1α-Hydroxycorticosterone as a Unique Corticosteroid in Elasmobranchs

The physiological role of the interrenal gland in teleosts has been studied in greatest detail in the eel, *Anguilla* spp. (Sandor et al. 1966; Butler and Langford 1967; Henderson and Chester Jones 1967; Sandor et al. 1967; Hirano and Utida 1968; Hirano 1969; Hirano and Utida 1971). In eels, interrenalectomy is facilitated because of the peculiar distribution of the interrenal gland. The gland is located in the left and right postcardinal veins accompanying a small tissue mass of elongated head kidney (Chester Jones et al. 1964; Butler and Langford 1967; Butler et al. 1969). In other teleosts, the interrenal gland is situated around the postcardinal veins, and branches occur within the relatively large head kidney tissue. Extirpation of this portion of the cardinal vein, with the interrenal gland attached, is practical in the eels. Mayer et al. (1967) performed an interrenalectomy on the European eel, *A. anguilla*, and found that the glandless eels did not survive in seawater for more than about 48 hours. A remarkable elevation of plasma concentrations of both sodium and

Table 2.
Weight of rectal glands in some elasmobranchs (Oguri 1981).

Species	Body weight	Rectal gland Length (cm)	Rectal gland Weight (g)	Rectal gland wt. (mg) /100 g body wt.
Bullhead shark[a]	160	0.5	0.04	25.0
Heterodontus japonicus	430	0.65	0.06	14.0
Small-spotted catshark	255	0.9	0.05	19.6
Scyliorhinus canicula	349	0.9	0.09	25.8
	400	1.1	0.05	12.5
	406	1.2	0.10	24.6
	439	0.9	0.11	25.1
	483	1.4	0.10	20.7
	618	1.6	0.13	21.0
	685	1.5	0.15	21.9
	709	1.1	0.11	15.5
	780	1.1	0.13	16.7
Tiger shark	37,650	8.5	6.1	16.2
Galeocerdo cuvieri	41,730	10.8	8.2	19.7
	273,060	15.8	30.8	11.3
Blacknose shark *Carcharhinus acronotus*	8,390	5.4	1.1	13.1
Bull shark *Carcharhinus leucas*	195,950	9.8	15.9	8.1
Blacktip shark	3,175	3.0	0.55	17.3
Carcharhinus limbatus	6,350	2.9	0.6	9.4
	22,230	3.2	1.5	6.7
	29,940	5.4	3.0	10.0
Spinner shark	3,290	3.1	0.5	15.2
Carcharhinus brevipinna	7,480	3.8	0.7	9.4
	8,505	4.1	0.7	8.2
Lemon shark	7,820	3.3	0.7	9.0
Negaprion brevirostris	118,840	7.3	12.0	10.1
Bonnethead shark	650	2.1	0.15	23.1
Sphyrna tiburo	990	2.5	0.2	20.2
	2,270	2.8	0.35	15.4
Leopard shark[a]	1,100	1.8	0.3	27.3
Triakis scyllia	1,700	1.9	0.3	17.6

[a] unpublished data.

chloride occurred, resulting in death. Cortisol (Fig. 1) is known to be the main corticosteroid in teleosts (Idler and Truscott 1972; Bentley 1982). Interrenalectomized eels survived if injected with cortisol, which normalized the reduced sodium turnover rate (Mayer et al. 1967). Cortisol is apparently a sodium-excreting hormone in seawater eels.

Interrenalectomy is performed more easily in chondrichthyans because the gland is close to, but separated from the kidney (Chester Jones 1976). However, interrenalectomy in elasmobranchs induces no statistically significant changes in blood electrolyte concentrations (Hartman et al. 1944; Idler and Szeplaki 1968). 1α-hydroxycorticosterone (Fig. 1) is the major corticosteroid in elasmobranchs (Idler and Truscott 1966, 1967, 1972; Butler 1973; Bentley 1982). However, the physiological role of 1α-hydroxycor-

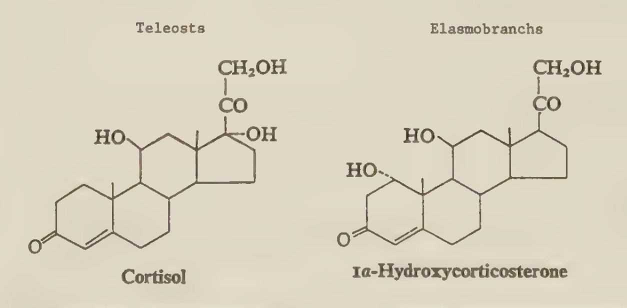

Figure 1.
Principal corticosteroid hormones in fishes (Bentley 1982).

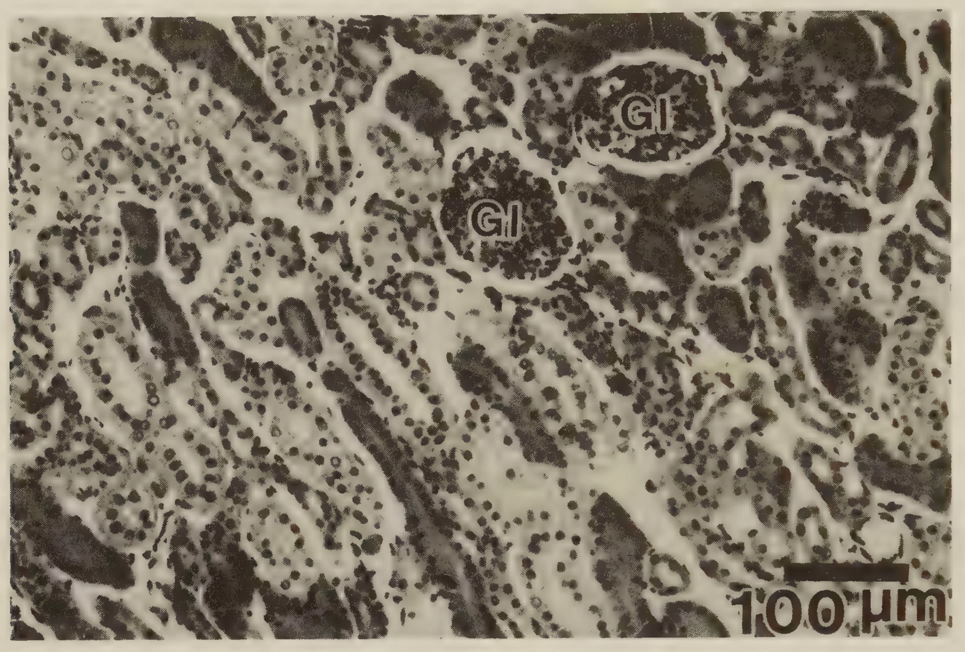

Figure 2.
A paraffin section (6 μm) of kidney tissue of *Potamotrygon* sp., prepared with Helly's fluid fixation, Mayer's acid hemalum, and eosin stain. Gl: glomerulus.

ticosterone in elasmobranchs has not been elucidated. Recently, Hazon and Henderson (1984) measured the peripheral plasma concentrations, metabolic clearance rates (MCR) and blood production rates (BPR) of 1α-hydroxycorticosterone of the catshark, *Scyliorhinus canicula*, in an environment of reduced osmolarity (90, 80, 70, 60, and 50% seawater) and confirmed the increase in plasma concentrations, MCR, and BPR of this hormone, together with the decline of plasma osmolarity, sodium, chloride, and urea concentrations. These results suggest that this unique vertebrate hormone perhaps governs the homeostasis of plasma composition, particularly with respect to urea.

The Kidney Structure of Ureosmotic Vertebrates

It is well known that the plasma osmolarity of marine elasmobranchs is a little higher than that of seawater (Pang et al. 1977). This is in remarkable contrast to marine teleosts where plasma osmolarity is about 370 mOsm/kg (Pang et al. 1977). The urea concentration in the blood plasma of marine elasmobranchs is about 2,000 to 2,500 mg/100 mL (Smith 1951), and this high concentration contributes to the elevation of plasma osmolarity in elasmobranchs. The high blood-urea concentration is in part due to high urea production in the elasmobranch liver. The activities of enzymes of the urea cycle are at high production levels when compared to teleosts which are ammonotelic animals (Huggins et al. 1969). Furthermore, the elasmobranch gill shows a very low permeability to urea in contrast to the teleostean gill (Smith 1951; Boylan 1967; Pang et al. 1977).

The elasmobranch kidney actively reabsorbs urea (Smith 1951; Kempton 1953; Boylan 1972). This is unique. The kidneys of most other vertebrates excrete urea instead of retaining it (Smith 1951). In conjunction with this physiological characteristic, the kidney structure of elasmobranchs is very complicated (Fig. 2). This complexity of the elasmobranch nephron has been reported in the greater cat shark, *Scyliorhinus stellaris* (Borghese 1966), and in the little skate, *Raja erinacea* (Deetjen and Antkowiak 1970; Stolte et al. 1977; Lacy et al. 1985; Hentschel et al. 1986). In contrast, the kidney structure of teleosts is rather simple (Hickman and Trump 1969) and nephron components such as neck, both proximally convoluted and distally convoluted segments, are easily distinguishable under light microscopy. In elasmobranchs, the nephron architecture is very intricate and further detailed investigations are needed.

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Ecology of Bacteria in Shark Tissue

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ABSTRACT

Healthy, free-ranging sharks captured and sampled for bacteria at Bimini, Bahamas, have been shown to contain, as autochthonous biota, primarily *Vibrio* spp. and *Clostridium* spp. The majority of the shark isolates from these two genera were proteolytic, owing, most likely, to the low carbohydrate content of the tissues and organs as well as the dietary intake of the shark hosts. Because sharks have a high tissue urea level, the isolates from both genera were checked for urease; the *Vibrio* spp. were 60% positive for urease. Subsequently, a study of liver homogenates from two carcharhinid sharks demonstrated that bacteria in the tissues were responsible for mineralization of ^{14}C-labeled urea, supporting the hypothesis that ureolytic bacteria in sharks decompose urea *in situ*. Commensally, *Clostridium* spp. could lend their amino acid fermentation end products to the *Vibrio* spp. as usable nutrients for assimilation or, in the case of gaseous H_2, as reducing power, thereby removing clostridial toxic wastes. Cohabitation of bacteria with their shark hosts is a unique system and further study will lead to a much better understanding of this unusual relationship and shark physiology.

An episode of dying sharks at the National Aquarium in Baltimore, MD, and the subsequent isolation of two potentially pathogenic *Vibrio* strains, has led to a major study of the bacterial biota of healthy, free-ranging neritic sharks (Grimes et al. 1984). Tissues and organs in the healthy sharks, areas considered sterile in other vertebrates, have been found to contain from 10^2 to 10^5 bacteria per gram (Grimes 1989). Several bacterial genera have been represented, with *Vibrio* spp. as the predominant gram-negative, facultative organisms and *Clostridium* spp. as the predominant anaerobes. These bacterial strains cohabit healthy sharks in a balanced or steady state until the shark becomes compromised. The opportunistic pathogenic bacteria, normally held in check, can flourish, create a disease condition, and eventually cause death.

It is obvious that a unique habitat exists in shark tissues and organs; a habitat that includes the coexistence of bacteria with these tissues without apparent detriments. What relationship bacteria have with sharks, or what benefits sharks may accrue from autochthonous bacteria, have yet to be determined. I will use the following review and recent data to address these questions.

Review

Infectivity

Bacteria considered to be potential or opportunistic pathogens may associate with or colonize (infect) eucaryotic cells without causing a disease state. The pathogenicity of these organisms does not become apparent until the right conditions exist. Also, the autochthonous biota of a eucaryotic system maintains a steady state, keeping potential pathogens in check and preventing these pathogens from overgrowth and from invading surrounding cells and/or tissues, which could ultimately lead to disease. Although the autochthonous biota may contain opportunistic pathogens, other potential pathogens could be introduced into the host at any time. Depending on the circumstances of infection, these newly introduced pathogens may cause disease, or they may be removed by the host's defense system, or the autochthonous biota may keep these bacteria in check. Therefore, isolating potential pathogenic bacteria from a host does not prove pathogenesis; it is only suggestive.

In order to show an organism's pathogenicity, one must introduce the pathogen into a susceptible host and that host must develop clinically observable disease. Two potentially pathogenic bacterial strains, isolated from a diseased sandbar shark, *Carcharhinus plumbeus* (Nardo), which had died in captivity, were tested for pathogenicity by this method (Grimes et al. 1984).

Results of the study were surprising (Grimes et al. 1985a). The potential pathogens, *Vibrio carchariae* and *Vibrio damsela*, inoculated into healthy lemon sharks, *Negaprion brevirostris* (Poey), were not lethal for these sharks as suspected. The shark became infected but recovered. Repeating the experiment on a physiologically compromised lemon shark proved lethal. It was concluded that healthy lemon sharks are susceptible to infection with *Vibrio carchariae*, but do not succumb to clinical disease or death unless compromised (e.g., stressed).

Table 1.
List of sharks sampled for microbiological evaluation.

Common name	Scientific name
Blacktip shark	*Carcharhinus limbatus* (Valenciennes) 1841
Sandbar shark	*Carcharhinus plumbeus* (Nardo) 1827
Tiger shark	*Galeocerdo cuvieri* (Lesueur) 1822
Nurse shark	*Ginglymostoma cirratum* (Bonnaterre) 1788
Sixgill shark	*Hexanchus griseus* (Bonnaterre) 1788
Lemon shark	*Negaprion brevirostris* (Poey) 1868
Caribbean sharpnose shark	*Rhizoprionodon porosus* (Poey) 1861
Spiny dogfish	*Squalus acanthias* (Smith and Radcliffe) 1912

Culture, Isolation, and Characterization

The next phase of study involved culturing healthy, free-ranging neritic sharks. Tissue and organ samples from more than 50 neritic sharks, comprising eight species (Table 1), were examined (Fig. 1). Duplicate samples were prepared and cultured for anaerobic bacterial isolation (Fig. 2).

Results from preliminary isolation and characterization demonstrated another unexpected phenomenon. All tissues and organs, excepting blood, contained bacteria, both facultative and anaerobic (Table 2).

The presence of bacteria in tissues and organs normally considered sterile surprised Grimes and his colleagues (Grimes et al. 1985b). Subsequent samplings of neritic sharks proceeded with utmost care in aseptic handling and collection. Particular care was taken to sample only uninjured sharks captured live, and aseptic sampling of sacrificed specimens was completed within 30 minutes of boating the shark. These precautions were taken to insure that the bacteria cultured were truly autochthonous flora and not contaminants.

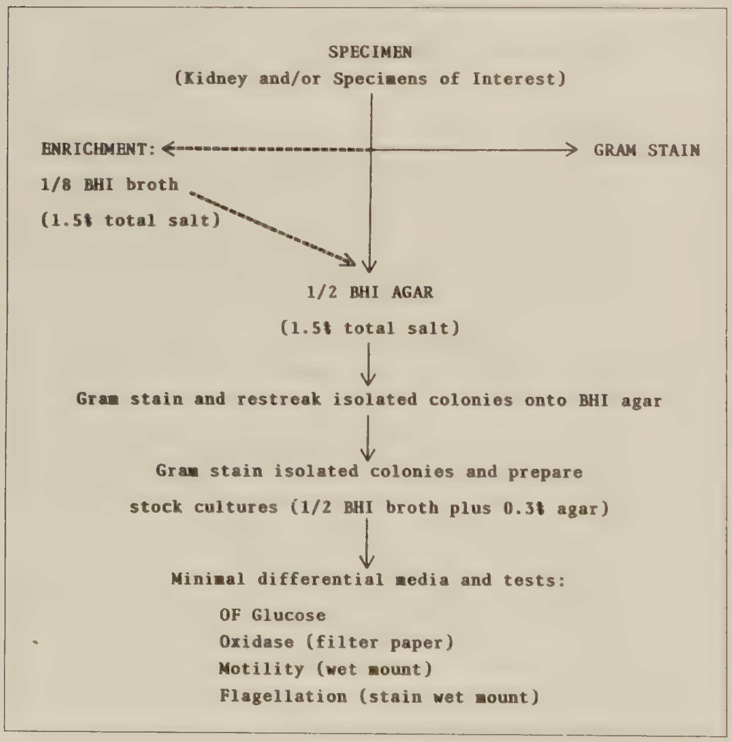
SPECIMEN
(Kidney and/or Specimens of Interest)
ENRICHMENT:
1/8 BHI broth
(1.5% total salt)
GRAM STAIN
1/2 BHI AGAR
(1.5% total salt)
Gram stain and restreak isolated colonies onto BHI agar
Gram stain isolated colonies and prepare
stock cultures (1/2 BHI broth plus 0.3% agar)
Minimal differential media and tests:
OF Glucose
Oxidase (filter paper)
Motility (wet mount)
Flagellation (stain wet mount)

Figure 1.
Sampling protocol for isolating gram-negative, facultative anaerobic bacteria from shark specimens (Baumann et al. 1984; West and Colwell 1984). BHI = brain heart infusion medium; OF = oxidation/fermentation medium.

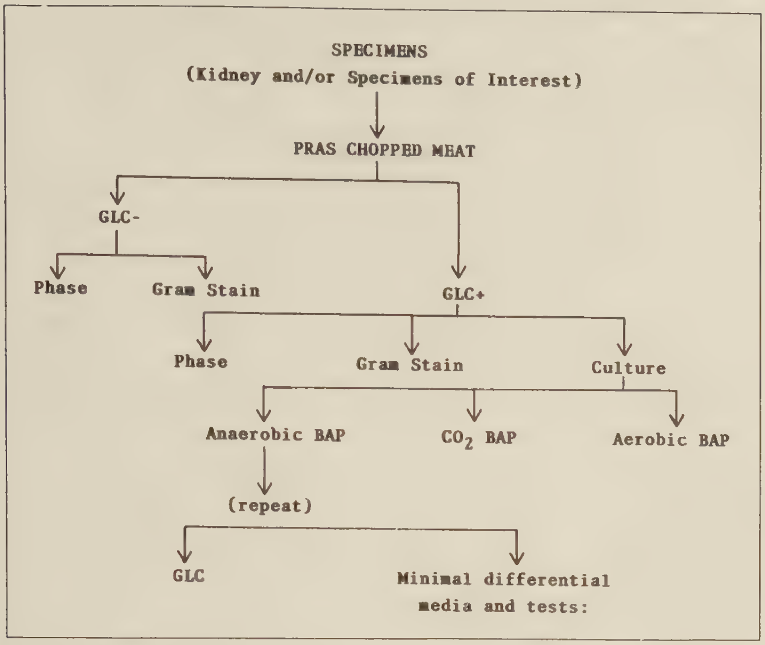

Figure 2.
Sampling protocol for isolating anaerobic bacteria from shark specimens (Cato et al. 1986; Holdeman et al. 1977). BAP = blood Agar Plates; GLC = Gas-Liquid Chromatography; PRAS = prereduced anaerobically sterilized.

Culture and isolation techniques were the same as those described previously (Figs. 1 and 2). Bacteria, again, were isolated from all tissues and organs sampled (Grimes et al. 1985b; Youngren-Grimes, unpubl. data). It was determined that *Vibrio* (59 out of 78 purified strains) and anaerobic *Clostridium* (29 out of 31 purified strains) were the predominant genera isolated. Characterized strains in these two genera tended to be proteolytic.

Numerical Taxonomy Studies

Using phenotypic characterization of bacterial strains isolated from sharks, 107 of these strains were identified to genus level and 48 to species level (Grimes et al. 1985a; Youngren-Grimes, unpubl. data). However, there were greater than 150 gram-negative, oxidase-positive isolates that could not be conclusively characterized to a genus. In Grimes' next study, the results of phenotypic characterization of 197 isolates were analyzed by means of both clustering and ordination, e.g., numerical taxonomy (NT). A second NT analysis was performed on the *Clostridium* isolates (29) in order to identify these bacteria to species level.

Table 2.
Distribution of bacteria in specific shark samples.

Mouth/Teeth *Clostridium* spp. *Photobacterium* spp. *Proteus* spp. *Vibrio alginolyticus* *Vibrio carchariae* *Vibrio furnissii* *Vibrio* spp.	Spiral valve *Aeromonas* spp. *Clostridium* spp. *Escherichia coli* *Pleisiomonas shigelloides* *Vibrio damsela* *Vibrio harveyi* *Vibrio* spp.	Liver *Vibrio carchariae* *Vibrio harveyi* *Vibrio* spp.
Kidney *Fusobacterium* sp. *Vibrio damsela* *Vibrio furnissii* *Vibrio* spp.	Stomach/Duodenum *Aeromonas* spp. *Closridium* spp. *Vibrio alginolyticus* *Vibrio* spp.	Pancreas *Clostridium* spp. *Vibrio harveyi* *Vibrio* spp.
Spleen *Fusobacterium* sp. *Vibrio harveyi* *Vibrio* spp.	Rectum/Anus/Cloaca *Aeromonas* spp. *Vibrio harveyi* *Vibrio* spp.	Esophagus *Aeromonas* spp. *Clostridium* spp. *Vibrio* spp.
Gill slit *Vibrio furnissii* *Vibrio harveyi* *Vibrio* spp.	Eye *Vibrio alginolyticus* *Vibrio* spp.	Gallbladder *Vibrio damsela*

The NT approach used was to calculate similarities with the Jaccard equation. This approach was followed by clustering the operational taxonomic units (OTU) with the unweighted pair group mathematical averaging method as described by Sneath and Sokal (1973). Materials and methods used for phenotypic characterization of each OTU have been described elsewhere (West and Colwell 1984; West et al. 1986; Holdeman et al. 1977). Although this approach portrays only 50 to 60% of the relatedness between OTU, it was expected that there would be significant clustering, especially among the reference strains used. What Grimes and Youngren-Grimes (unpubl. data) found was that very few isolates clustered with reference strains (7). A significant number (189 out of 197) of unknown bacteria could not be identified by this technique (Table 3). This phenomenon was repeated in the anaerobic clustering analysis. Only five of the unknown strains clustered with a known reference strain (Table 3). At first these

Table 3.
Summary of numerical taxonomic analysis of gram-negative, faculative, anaerobic bacteria isolated from sharks.

				Unidentified	
Total strains	Reference strains	Unknown strains	Identified strains	Clusters	Not clustered
Gram-negative, facultative anaerobes					
236	39	197	Phenon 1 *V. alginolyticus* (17)	28 Phena (108)	81
			Phenon 5 *V. parahaemolyticus* (6)		
			Phenon 8 *V. harveyi* (2)		
			Phenon 9 *V. carchariae* (11)		
			Phenon 18[a] *V. cholerae* (6)		
			Phenon 19 *V. tubiashii* (3)		
			Phenon 20 *V. fluvialis* (2)		
Anaerobes					
43	14	29	Phenon 2 *C. sporogenes* (5)	3 Phena (6)	18

[a] The 6 strains clustered were all *V. cholerae* reference strains, no unknowns.

results seemed quite surprising. However, the uniqueness of near homogeneous bacterial colonization of sharks offers some explanation. When colonizing a host, bacteria will adapt to the substrates available from that host with respect to their carbon and energy needs and other necessary growth factors. If the substrates are unusable or the competition is too great, bacteria will either be eliminated or remain in a nongrowth state until conditions improve (Kjelleberg et al. 1987; Barnes and Mead 1986; Davis and Robb 1985; Fletcher and Floodgate 1985; Amy and Morita 1983). Adaptation to the substrates available in the host is expressed as phenotypic traits. The environmental isolates may be closely related genetically to reference strains, but depending on the habitats of each, may be phenotypically very different. In the present case, the reference strains were not of shark origin and simply may be expressing phenotypic characteristics associated with their environmental origin. It would, therefore, be more significant to apply ordination analysis to ribosomal sequences of the shark isolates and the reference strains (MacDonell et al. 1986).

Recent Data

Urea Hydrolysis

During characterization testing, Grimes et al. (1985b) found that 60% of the *Vibrio* spp. isolated from shark tissues were urease positive. This high incidence of urea hydrolysis is unusual, when compared to the finding of West et al. (1986) who reported less than 12% of the genus *Vibrio* to be urease positive. The ability to hydrolyze urea to CO_2 and NH_3 was hypothesized as a possible mechanism for controlling shark tissue storage and flux of urea. Knight et al. (1988), in a study using radio-labeled urea, determined that bacterial hydrolysis occurs in tissues of free-ranging neritic sharks.

In essence, as reported by Knight et al. (1988), blood homogenates from two carcharhinid sharks, *Galeocedo cuvieri* and *Negaprion brevirostris*, showed no significant difference between saline (control), 0/129 (a bacteriostatic agent), or antibiotic treatments (Figs. 3 and 4). Liver homogenates did, however, demonstrate a significant difference ($P < 0.05$) between saline and 0/129 or antibiotic treatments. The saline treated liver homogenates, from each shark, increased to the same level of ^{14}C-labeled mineralization at the end of 48 hours, i.e., 1.3 logs higher than samples treated with antibiotic.

Mineralization of ^{14}C-labeled urea to CO_2 in the liver homogenates, but not in the blood, indicates that ureolytic bacteria are present and active in the liver but not in the sterile circulatory system. This ureolytic activity in shark liver provides evidence that autochthonous bacterial biota in shark tissue may play a significant role in shark urea homeostasis. In addition, the hydrolytic CO_2 may act as a buffer in the tissues, maintaining a slightly alkaline environment.

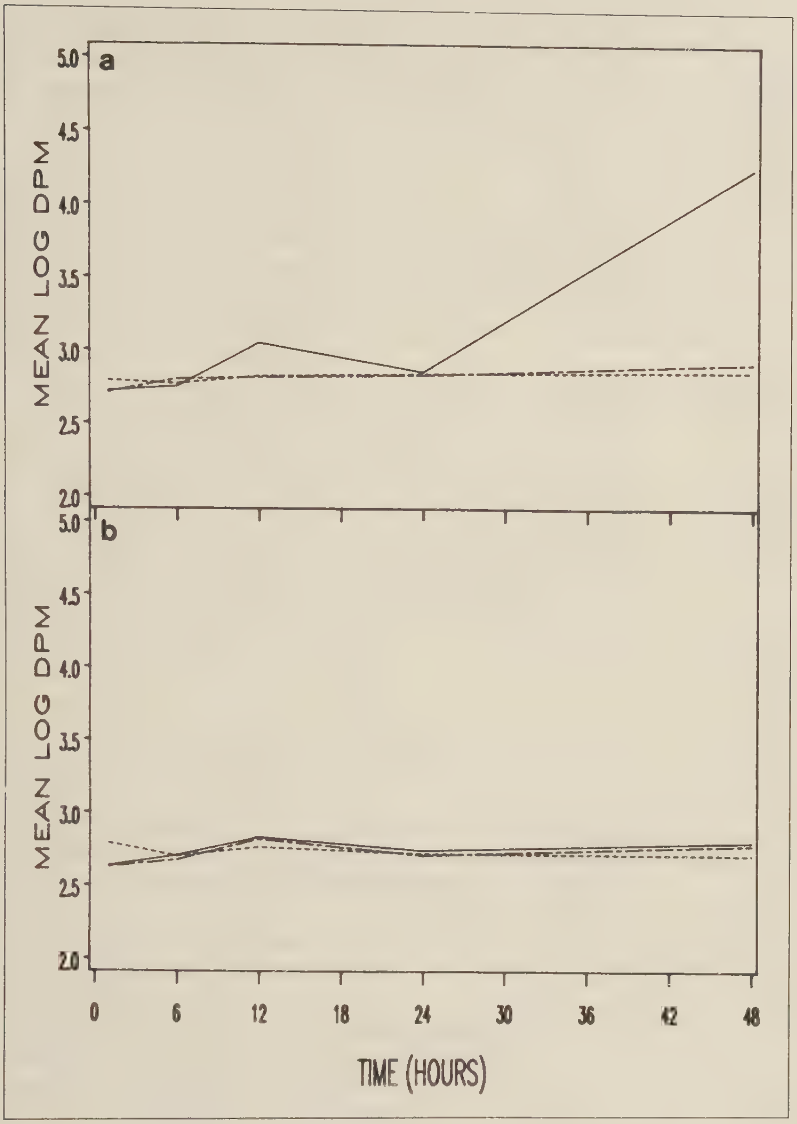

Figure 3.
Mean $\log_{10}$ disintegrations per minute (DPM) in NaOH vs. time of incubation of lemon shark (a) liver and (b) blood homogenates with ^{14}C-labeled urea. Homogenates were treated with saline (—), 0/129 (- - -), and ampicillin (— - —). Reproduced from Knight et al. (1988), with permission.

Physiology and Commensalism

Because of the carnivorous nature of elasmobranchs, it was not surprising to find that the majority of the isolated *Vibrio* and *Clostridium* spp. secreted proteolytic enzymes capable of degrading or hydrolyzing proteins into small peptides or into amino acids. These catabolites were then used as necessary nutrients for biomass production or as necessary growth factors.

Proteolytic clostridia, when present in a carbohydrate-free environment, are capable of fermenting amino acids, purines, pyrimidines, and other nitrogenous organic compounds by a unique pathway, the Stickland reaction, involving deamination (Barnes and Mead 1986). During the Stickland reaction one amino acid serves as an electron donor (oxidized by nicotinamide adenine dinucleotide) and a second amino acid serves as an electron accepter (reduced by dihydrogen nicotinamide adenine dinucleotide formed during the oxidation step). The end products of this reaction, e.g., acetic acid, may also be used as substrates for other energy-yielding catabolic pathways. Other examples of fermentation end products include short chain fatty acids, NH_3, alcohols, and gases (H_2, CO_2).

It is possible that *Vibrio* spp. may benefit from clostridial fermentation while ultimately improving the environment of the shark for *Clostridium* spp. Vibrios would preferentially use any available carbohydrate in the gut or tissues of sharks, scrubbing oxygen in the process. This would lower the oxidation-reduction potential (Eh) of the environment, creating a more anaerobic setting for the clostridia. Without carbohydrates, clostridial amino acid fermentation would proceed, supplying many fermentation products which could be used by the vibrios as alternative carbon and energy sources, thereby removing clostridial wastes from the shark tissues. In another mutual advantage, vibrios could scavenge excess reducing power of clostridia,

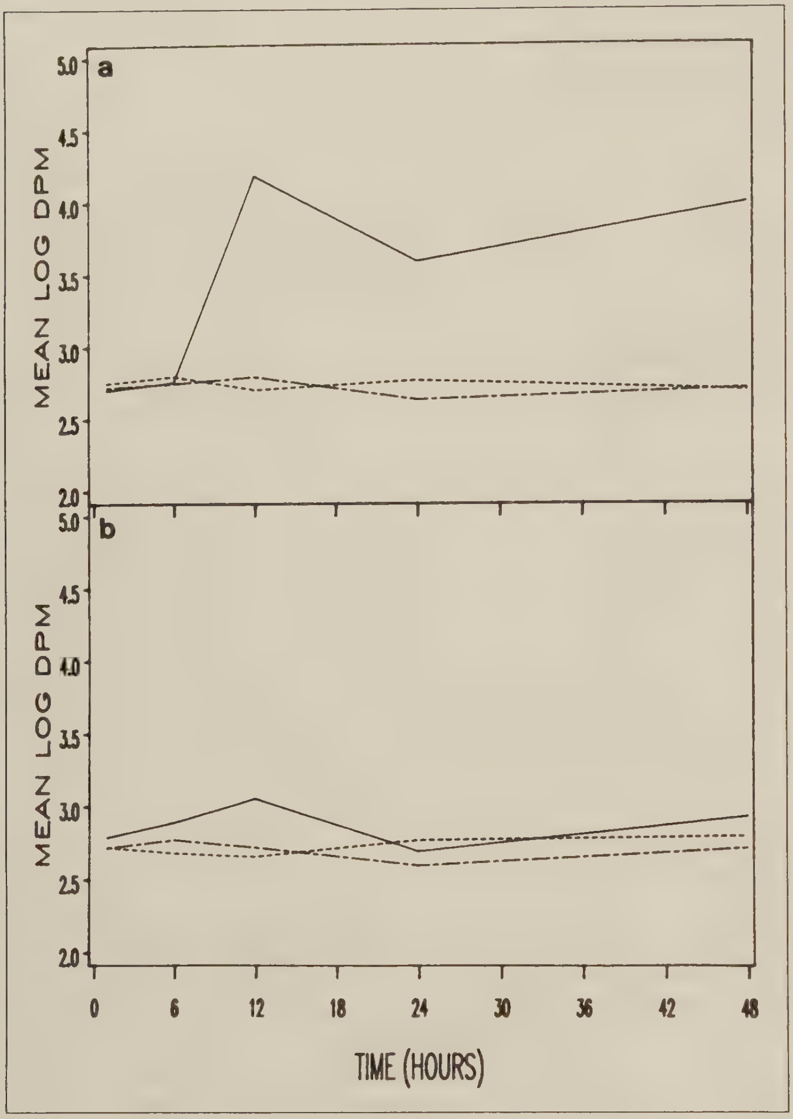

Figure 4.
Mean $\log_{10}$ disintegrations per minute (DPM) in NaOH vs. time of incubation of tiger shark (a) liver and (b) blood homogenates with ^{17}C-labeled urea. Homogenates were treated with saline (—), 0/129 (- - -), and ampicillin (— - —). Reproduced from Knight et al. (1988), with permission.

as gaseous H_2. The H_2 then could be employed by vibrios as the primary electron donor in their anaerobic respiration.

Although the genus *Vibrio* is not known to ferment amino acids (Baumann et al. 1984), many *Vibrio* strains isolated in sharks have secreted proteolytic enzymes capable of protein degradation; the peptides and amino acids of degradation could, most likely, be used as growth factors for these bacteria.

Besides proteolytic enzymes, shark isolates from both genera secrete or produce other enzymes capable of hydrolysis or degradation of substrates provided by the shark, e.g., muscle. To the ecologist or clinician, many of these enzymes are regarded as virulence factors or as mechanisms for invasion and dissemination (Grimes et al. 1989). To the bacteria, these enzymes offer a means of degrading substrates for sources of carbon, free energy, nitrogen (usually in the form of NH_3), and growth factors, thereby providing nutrients for assimilation.

Ammonia, whether from catabolism or other sources, is a very versatile and necessary nitrogenous compound in the bacterial world. It serves as a nitrogen source, as a substrate, as an amine group to be incorporated into bacterial metabolites and other synthesized organic compounds, or as an end product of metabolism, to name a few examples.

Both vibrios and clostridia readily use NH_3 as a source of nitrogen or as an amine group in biosynthesis. They also produce NH_3 as an end product (urea hydrolysis and amino acid deamination). Possibly the NH_3 released by bacteria into shark tissues could aid in maintaining the slightly alkaline conditions found in the shark tissues, benefiting both the bacteria and homeostasis in the shark. Clostridial deaminases are produced optimally at alkaline pH values (Barnes and Mead 1986). For *Vibrio* spp., the released NH_3 could create an alkaline microenvironment (~ pH 8.0–8.5) that would allow the bacteria to shift into a more efficient respiratory-linked Na^+-motive pump that could drive Na^+-dependent flagellar motion and ATP synthesis (Dimroth 1987).

Concluding Remarks

Recovering bacteria from shark tissues and organs is unusual. One would expect to find bacteria in the gut, not in tissues and organs. Isolating these potential pathogens without evidence of clinical disease suggests a commensal cohabitation with sharks.

The two prominent genera *Vibrio* and *Clostridium*, cultured as autochthonous flora of neritic sharks, are ideally suited for survival in unusual and varied nutrient environments (Kjelleberg 1987; Barnes and Mead 1986; Cato et al. 1986). The shark, too, appears adapted for keeping its bacterial residents in a balanced or steady state. Knowing more about the bacterial-host relationship of sharks could also lead to a better understanding of the general physiology of sharks.

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Review of Human Pathogenic Bacteria in Marine Animals with Emphasis on Sharks[1]

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ABSTRACT

Bacteria belonging to the genus *Vibrio* were demonstrated as etiologic agents of disease in captive sharks, following their isolation from a dead sandbar shark, *Carcharhinus plumbeus*, and from experimentally infected lemon sharks, *Negaprion brevirostris*. Studies were expanded to healthy, free-ranging sharks captured and sampled for bacteria at Bimini, Bahamas. The bacterial flora of 28 neritic sharks, comprising five species, were examined. All 28 sharks were colonized with bacteria, primarily the genus *Vibrio*. All tissues and organs sampled contained *Vibrio* spp., including liver, spleen, kidney, eye, mouth, skin, pancreas, intestine, stomach, gall bladder, gill slits, and fetuses (from a pregnant sharpnose). The conclusion, based on over 300 bacterial isolates from over 50 healthy sharks, is that sharks contain an autochthonous flora in most tissues and organs. The bacteria typically number between 10^2 and 10^5 bacteria per gram of tissue except blood, which is free from both aerobic and anaerobic bacteria. Human pathogens among the isolates included *V. alginolyticus*, *V. parahaemolyticus*, *Listonella damsela*, and *Clostridium* spp. While their ecological niche remains an enigma, it is clear that bacteria in healthy sharks can derive nutrients from elasmobranchs and, under conditions of stress to the host, cause death. Equally clear is the fact that when used as food, shark meat must be thoroughly cooked to destroy potential pathogens. If not properly cooked, pathogens such as *V. parahaemolyticus* could initiate gastroenteritis.

Introduction

In 1982, the National Aquarium in Baltimore experienced unusually high morbidity and mortality among their display sharks and provided the author samples from a dead sandbar shark, *Carcharhinus plumbeus*. Two vibrios were isolated (Fig. 1), *Vibrio carchariae* from kidney and *Vibrio damsela* from liver samples (Grimes et al. 1984a). It was subsequently demonstrated that each isolate was capable of infecting and causing disease in healthy lemon sharks, *Negaprion brevirostris* (Grimes et al. 1985a). In subsequent studies, *V. carchariae* was found to have a unique 5S ribosomal RNA sequence (MacDonell and Colwell 1985a), confirming the original description (Grimes et al. 1984a) of it as a new species. *V. damsela* was subsequently placed into a new genus, *Listonella* (MacDonell and Colwell 1985b).

Examination of apparently healthy, control lemon sharks that had been inoculated intraperitoneally with sterile saline during reinfectivity studies (Grimes et al. 1985a) revealed the presence of potentially pathogenic *Vibrio* species. Consequently, additional healthy, free-ranging sharks were examined, and *Vibrio* species, as well as other pathogenic bacteria, were found to reside in shark tissue (Grimes et al. 1985b). This unusual finding suggests that sharks are a potential health risk to humans, and this review will discuss the risk in context with other marine animals known to harbor human pathogens. In addition, the ecology of elasmobranch-borne pathogens will be discussed.

Human Pathogens in Marine Animals

Shellfish frequently become colonized with human pathogens (Table 1). In past years, typhoid fever, caused by *Salmonella typhi*, was the major disease associated with consumption of contaminated bivalve molluscs. In recent years, however, *S. typhi* has been virtually eliminated as a shellfish contamination problem, in part due to effective bacteriological monitoring of shellfish and shellfish waters and beds. Today, viruses are the major problem associated

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[1] Contribution No. 225 from the Jackson Estuarine Laboratory.

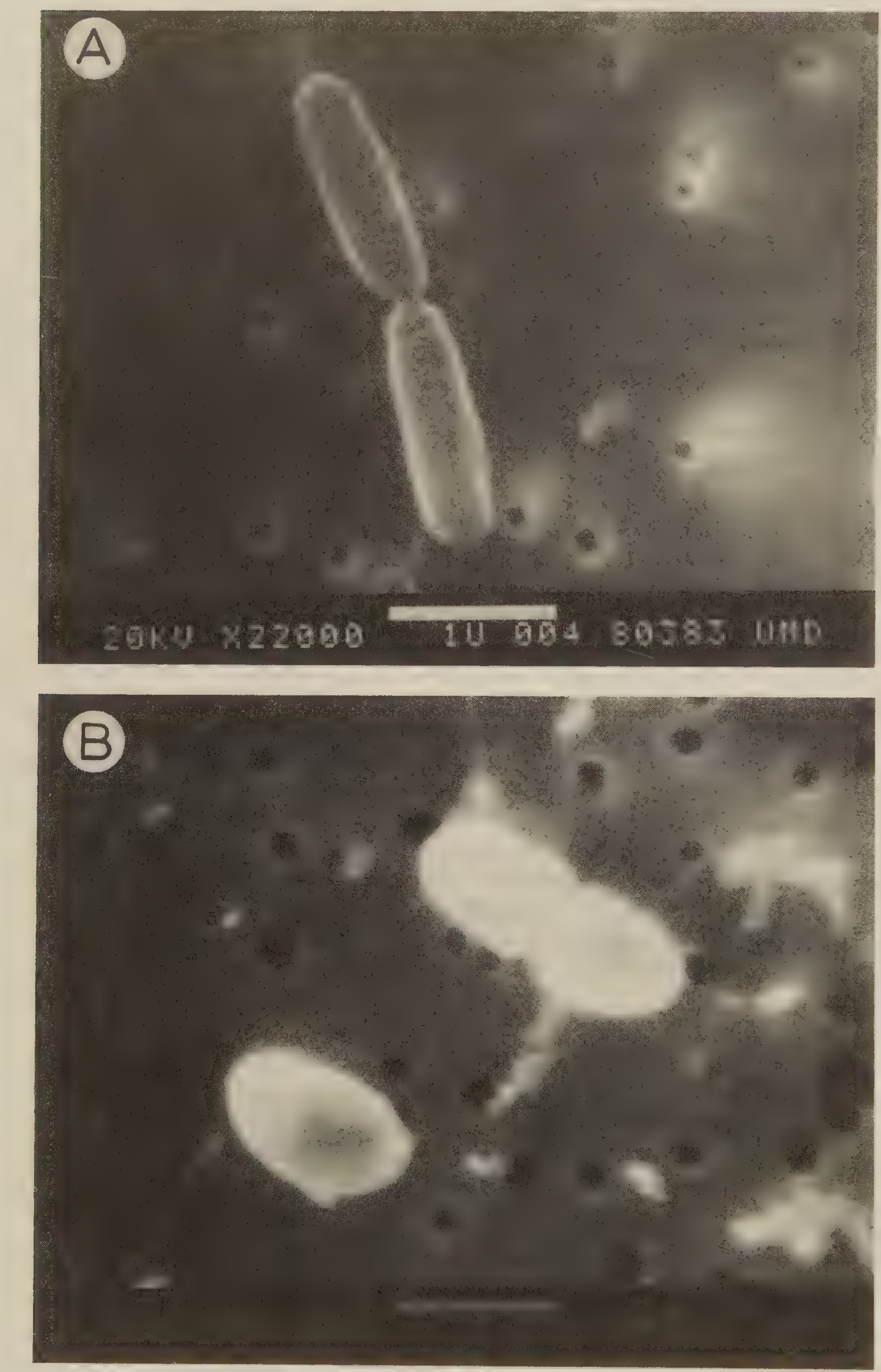

Figure 1.
Scanning electron micrographs of (A) *Vibrio carchariae* (× 22,000) and (B) *Listonella damsela* (× 21,000) grown in MSWC broth (see Grimes et al. 1984a).

Table 1.
Human pathogens frequently associated with shellfish.

Norwalk virus
Picornaviruses
Aeromonas hydrophila
Campylobacter jejuni
Clostridium spp.
Escherichia coli
Plesiomonas shigelloides
Salmonella spp.
Vibrio cholerae
Vibrio parahaemolyticus
Vibrio vulnificus
Gonyaulax spp.
Ptychodiscus brevis
Pyrodinium monilatum

with shellfish, and disease incidence derived from consumption of virus-contaminated shellfish is on the increase. Table 2, adapted and updated from Goyal (1984), lists the more recent outbreaks of shellfish-borne disease. Clearly, most cases have been caused by viruses.

Bony fish also carry microorganisms which are potentially pathogenic for humans. However, when human pathogens are detected in bony fish, they are usually transients, present on the skin or in the gut; very seldom are

Table 2.
Recent outbreaks of disease derived from shellfish[a]

Shellfish	Agent[b]	Location	No. of cases	Citation
Oysters	Norwalk	Australia	2,000	Murphy et al. 1979
Oysters	Norwalk	Australia	150	Grohman et al. 1981
Mussels	HAV	England	41	Bostock et al. 1979
Shrimp	Vp	Louisiana	600	CDC 1972
Crabs	Vc	Louisiana	10	CDC 1978
Oysters	HAV	Alabama and Georgia	10	CDC 1979
Oysters	Norwalk	Florida	6	Gunn et al. 1982
Clams	Norwalk?	New York	150[c]	CDC 1982
Clams	Cj	New Jersey	18	Blaser et al. 1982
Clams	Cj	Japan	101	Itoh et al. 1982
Oysters	Vv	United States	24	Blake et al. 1979
Molluscs	Norwalk	New York	1,017[d]	Morse et al. 1986

[a] Adapted from Goyal (1984).
[b] HAV = Hepatitis A virus, Vp = *V. parahaemolyticus*, Vc = *V. cholerae*, Cj = *C. jejuni*, Vv = *V. vulnificus*.
[c] Represents 14 different outbreaks including cases of hepatitis.
[d] Represents 103 different outbreaks.

human pathogens found within deep tissues of bony fish and when they are detected the fish usually exhibit pathology.

Table 3 lists some of the human pathogens that are frequently encountered in bony fish specimens. It should be noted that most microorganisms on this list have a broad host range, in that they are not only pathogenic for humans and fish but also for other mammals, birds, and amphibians. The incidence of human morbidity caused by *Cryptosporidium* is becoming more frequent (Stibbs and Ongerth 1986). This protozoan appears to be widespread in nature, being present in fish (Dykova and Lom 1983; Pavlasek 1983). The resulting diarrhoeal disease is most common among immunodeficient persons (Stibbs and Ongerth 1986).

Marine mammals also carry human pathogens (Buck and Spotte 1986; Smith et al. 1978), some of which can cause serious disease in man and other terrestrial animals. Table 4 lists microorganisms frequently isolated from cetaceans and pinnipeds. Of the species listed, coagulase-positive staphylococci and *Vibrio* spp. are also ubiquitous in seawater, comprising over 1% and 60%, respectively, of randomly picked colonies isolated from seawater on marine agar (Grimes et al. 1984b). It is well documented that *Vibrio* spp. are autochthonous to marine and estuarine environments (Grimes et al. 1984b) and it appears that staphylococci are as well (Gunn and Colwell 1983). A 1987 outbreak of disease among marine mammals involved the deaths of over 300 bottlenose dolphins, *Tursiops truncatus*, from the northern Atlantic coast of the United States. Results of necropsies on several specimens demonstrated a secondary *Vibrio* involvement and findings that parallel our studies in sharks, e.g., skin lesions and septicemia.

Table 3.
Human pathogens frequently associated with bony fish.

Aeromonas spp.
Clostridium botulinum
Erysipelothrix rhusiopathiae
Mycobacterium marinum
Plesiomonas shigelloides
Pseudomonas aeruginosa
Salmonella spp.
Vibrio cholerae
V. alginolyticus
V. fluvialis
V. furnissii
V. parahaemolyticus
Listonella damsela
Clonorchis sinensis
Heterophyes heterophyes
Diphyllobothrium latum
Cryptosporidium

Table 4.
Human pathogens frequently associated with cetaceans and pinnipeds.

Actinomyces mallei
Caliciviruses
Coagulase + staphylococci
Clostridium chauvoei
Clostridium perfringens
Klebsiella pneumoniae
Leptospira interrogans
Neisseria mucosa
Nocardia spp.
Pasteurella multocida
Pseudomonas aeruginosa
Streptococcus pyogenes
Vibrio spp.

Risk of Contracting Human Disease from Marine Animals

Factors necessary for initiation of infectious disease in humans are listed in Table 5. Mode of transmission is, perhaps, the most critical factor, since all other factors are usually present in a given situation. It is for this reason that shellfish, primarily bivalve molluscs, constitute the

Table 5.
Key factors of infectious disease.

1. Infectious disease agent
2. Reservoir or habitat
3. Mode of transmission to host
4. Ability of agent to survive transmission
5. Portals of entry and exit
6. Susceptible host

most important source of water-borne disease in the United States today. Humans consume raw bivalves and, consequently, contract diseases. Transmission of pathogens from bottom sediment or seaweed surfaces to humans is not highly probable, and, hence, there are few reports of diseases deriving from such sources. However, as consumption of raw fish, seaweed, ''seasalt'', and other emerging marine foodstuffs increases, transmission of disease will become more frequent.

Human Pathogens in Sharks

The hypothesis that elasmobranchs carry an autochthonous bacterial flora throughout their various tissues was first proposed by Grimes et al. (1985b). This hypothesis is now based on a sampling regime that has included over 50 healthy, free-ranging neritic sharks collected from relatively pristine waters off the island of Bimini, Bahamas. Buck (1984) arrived at a similar conclusion after bacteriological examinations of skin, teeth, and gill surfaces and intestinal contents from 12 elasmobranchs taken from the Gulf of Mexico off Sarasota, Florida. Table 6 lists the shark species sampled to date, and Table 7 lists the tissue types examined and average bacterial concentrations in the various tissues. In general, blood is free from detectable bacteria, unless the shark has been severely compromised (e.g., stressed during capture) or is in a frank state of disease (Grimes et al. 1985b). Potential human pathogens isolated from various tissues and organs are listed in Table 8. Data presented in this table are a composite of all sharks sampled to date. The significance of *Clostridium* spp. present in

Table 6.
Sharks sampled for autochthonous bacteria.

Common name	Scientific name	Capture site
Blacktip shark	*Carcharhinus limbatus*	Bimini, Bahamas
Sandbar shark	*Carcharhinus plumbeus*	National Aquarium, Baltimore
Tiger shark	*Galeocerdo cuvieri*	Bimini, Bahamas
Nurse shark	*Ginglymostoma cirratum*	Bimini, Bahamas
Lemon shark	*Negaprion brevirostris*	Bimini, Bahamas
Sharpnose shark	*Rhizoprionodon porosus*	Bimini, Bahamas
Spiny dogfish	*Squalus acanthias*	Gulf of Maine
Sixgill shark	*Hexanchus griseus*	Bermuda

Table 7.
Densities of bacteria in selected shark tissues and organs[a].

	Lemon shark			
Organ/tissue	A	B	C	Average
Blood	0[b]	0	0	0
Muscle	0	$<10^5$	$<10^5$	$<7 \times 10^4$
Stomach	7×10^2	2×10^2	6×10^3	2.3×10^3
Intestine	2×10^4	$>10^6$	$>10^6$	7×10^5
Spiral valve	ND[c]	1×10^4	$>10^6$	$>5 \times 10^5$
Kidney	1×10^5	1×10^6	3×10^2	4×10^5
Spleen	ND	2	8×10^2	4×10^2
Liver	7×10^4	0	0	2×10^4

[a] Heterotrophic spread-plate colony count per gram of tissue on Marine Agar 2216 (Difco).
[b] 0 values represent no developed colonies after spread-plating 1.0 mL blood or 0.1 mL of a 1:5 dilution of muscle or liver, with extended (>21 d) incubation.
[c] ND = Not determined.

Table 8.
Human pathogens isolated from healthy sharks.

Aeromonas hydrophila
Clostridium botulinum
Clostridium perfringens
Clostridium sordellii
Clostridium tetani
Escherichia coli
Fusobacterium sp.
Listonella damsela
Plesiomonas shigelloides
Proteus spp.
Vibrio alginolyticus
Vibrio furnissii
Vibrio parahaemolyticus

shark tissue samples is discussed by Youngren-Grimes (1990). In progress, and not included in Table 8, is a numerical taxonomic study of 236 gram-negative, oxidase-positive strains of bacteria isolated from sharks captured in the coastal waters of Bimini (5 lemon, 1 blacktip, 1 sixgill, 4 nurse, and 4 tiger; see Table 6). The various phena are still being evaluated, but one interesting identification was that of a strain of *V. parahaemolyticus* isolated from a forearm shark bite wound sustained by one of the scientists while assisting with blood collection from a lemon shark (Grimes et al., in prep.). Such an infection was predictable, based on the findings of Buck et al. (1984). Other potentially pathogenic species identified in this numerical study were *V. alginolyticus*, *V. fluvialis*, *V. vulnificus*, and *L. damsela*.

In addition to direct isolations, substantial serological evidence of human pathogens in elasmobranchs has also been accumulated. Microagglutination experiments performed with heat-inactivated serum collected from healthy, free-ranging sharks and with members of the *Vibrionaceae* and *Aeromonadaceae* provided preliminary evidence of high antibody titers to several strains of pathogenic *Vibrio* spp. Pooled sera from six nurse sharks were then purified by DEAE (cellulose N, N-diethylaminoethyl ether) separation, followed by size exclusion with Sephadex G-200. The resulting purified protein had a molecular weight of $>$200,000, lost all agglutination activity upon treatment with 2-mercaptoethanol, and migrated through 10% polyacrylamide in a manner similar to human immunoglobulin M (IgM). These results strongly suggest that nurse sharks produce IgM in response to autochthonous pathogens such as *Vibrio carchariae* (Brayton et al., in prep.). Perhaps of greatest ecological significance was the observation that nurse sharks consistently possessed the highest antibody titers of all sharks ($\sim$1:1024), and that these high titers were frequently against *V. cholerae*, the classic agent of human cholera. Nurse sharks are bottom feeders, living on crustaceans and molluscs; both of these benthic invertebrates are natural habitats for *V. cholerae* (Hood et al. 1981; Huq et al. 1986).

It is now quite clear that elasmobranch tissues and organs, unlike those of bony fish, contain autochthonous bacteria, including potential human pathogens. Both direct isolation and serology support this hypothesis. Portals of entry have been previously discussed (Grimes et al. 1985b), and both the serological and direct isolation data support the hypothesis that sharks are continuously exposed to a variety of marine bacteria. These primitive fish have evolved an ability to co-exist with most of the potential pathogens, including the human pathogens. Only when sharks are compromised does this co-existence break down, and the sharks succumb to clinically evident disease.

Past studies with ^{14}C-labelled urea and anti-*Vibrio* antibiotics suggested that shark tissues are incapable of hydrolyzing urea. Instead, data revealed that the resident bacteria hydrolyzed urea, thereby benefiting their shark hosts by maintaining a relatively stable tissue urea concentration (Knight et al. 1988). Also of interest is a study of the ability of *V. carchariae* to decompose common shark biopolymers, especially connective tissue constituents (Grimes et al. 1989). The data collected showed that *V. carchariae* strains were capable of hydrolyzing chondroitin sulfate, hyaluronic acid, gelatin, and collagen and were also capable of using squalene as a pure carbon source. Obviously, such a hydrolytic repertoire would be of great benefit to *V. carchariae* as a colonizer and scavenger of shark tissue.

Conclusions

In conclusion, potential human pathogens are ubiquitous in marine animals, including elasmobranchs. These pathogens do not often cause disease in man, presumably because they lack a mode of transmission. However, increased reliance on the sea for food and recreation, combined with a concomitant increase in the disposal of anthropogenic wastes in the sea, increases the probability for human disease to occur, especially when one considers that fish are often consumed in a raw state, e.g., sushi, sashimi, and raw oysters. Obviously, consumption of raw fish, including raw shark meat, with an infective dose of a human pathogen (Table 8) could lead to gastroenteritis. Supportive of this statement are recent reports describing an increase in shellfish-borne diseases derived from the sea (Goyal 1984; Table 2). Clearly, continued introduction of human pathogens into the oceans of the world, along with nutrients to support growth of both introduced (allochthonous) and autochthonous microorganisms, will increase the probability of transmission (Grimes et al. 1986). Less clear is the role that these pathogens play after colonizing marine animals. Allochthonous human pathogens are probably transient, having little positive or negative effect on their temporary host. There are exceptions to this generalization of course, for example the calicivirus diseases of swine and marine mammals (Smith et al. 1978). Autochthonous bacteria capable of causing human diseases, on the other hand, fill a true niche in the marine environment. While the identity of this niche is not always clear, in some cases it appears to involve degradation, e.g., degradation of invertebrate chitin (Huq et al. 1986; Wortman et al. 1986) or shark tissue urea (Grimes et al. 1985b; Knight et al. 1988) by *Vibrio* species.

Acknowledgments

This review is dedicated to Samuel "Sonny" Gruber who has provided ship time, assistance in sample collection, and insight to a truly fascinating group of fishes, the sharks.

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Metazoan Parasites as Indicators of Elasmobranch Biology

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ABSTRACT

The biology of the four most frequently encountered metazoan phyla of elasmobranch parasites, including the Annelida, Nematoda, Platyhelminthes, and Arthropoda, is summarized. Specific examples of the major subgroups of parasites in each phylum are figured, and a generalized life cycle showing the involvement of the elasmobranch is presented for each. In addition, the phylum Acanthocephala and the phylum Mollusca are briefly discussed as only a few species parasitizing elasmobranchs are known from each. The use of parasites as indicators of the following six aspects of the biology of their elasmobranch hosts is treated: 1) movement and migrations, 2) feeding biology, both in general and with respect to size related changes in diet, 3) predators, 4) identification, 5) phylogeny, using A: direct inference from host specificity data, B: phylogenetic analysis of parasite presence/absence data, and C: phylogenetic analysis of parasite presence/absence data combined with phylogenetic analysis of the parasites; and 6) origins and ancient distributions. For each of these aspects attributes of parasites that are necessary for providing the information are discussed, and parasite groups possessing these attributes are identified. One or more examples is given in each case.

Introduction

Elasmobranch fishes host a variety of metazoan parasites including groups that are ectoparasitic (external parasites) such as the Monogenea, Annelida, Arthropoda, and Mollusca and groups that are endoparasitic (internal parasites) such as the Aspidocotylea, Digenea, Eucestoda, Nematoda, and Acanthocephala. The complex life histories of many of these parasite groups, as well as, in many cases, their tight host specificity and conspicuousness, endow them with the potential to be extremely informative as indicators of a number of aspects of the biology of their elasmobranch hosts. Discussions regarding the use of parasites as biological indicators for their hosts are frequently encountered in the literature (Kabata 1963; Kabata and Ho 1981; Manter 1966; Margolis 1965; Metcalf 1929; Sinderman 1957). Unfortunately, elasmobranchs are rarely the hosts featured in such discussions. It is therefore my primary objective in the present study to specifically address parasites of elasmobranchs and their use in inferring information about the biology of their elasmobranch hosts. I will begin by listing the various aspects of the biology of parasites about which it is important to have some knowledge, because the types of host information that can be inferred from parasites depend directly upon the biology of the parasites themselves. This will be followed by a discussion of the various groups of metazoan organisms that parasitize elasmobranchs along with some of the pertinent details of their biology. I will then elaborate on six features of elasmobranch biology about which parasites have the potential to supply information. For each of these six features I will indicate the parasite groups appropriate for obtaining this information and I will provide at least one example of each. Because of the relative infrequency with which acanthocephalans and molluscs occur as parasites of elasmobranchs, these two phyla will be excluded from consideration as parasite groups appropriate for obtaining host information.

Parasite Biology

In order for a parasite species to be maximally informative about its elasmobranch host, eight aspects of the parasite's biology should be considered including 1) Is the parasite ectoparasitic (external) or endoparasitic (internal)? 2) Does it possess only a single host species in its life cycle (monoxenous) or does it pass through a number of different host species during the course of its life cycle (polyxenous)? 3) If the parasite is polyxenous, is the elasmobranch the intermediate host (host in which larval development occurs) or the definitive host (host in which the parasite reaches sexual maturity)? 4) Does the parasite normally prefer a marine or a freshwater environment? 5) How does the parasite enter/find the elasmobranch host? For parasite species that pass through one or more hosts previous to the elasmobranch, this question is closely associated with the question: How does the parasite leave the host previous to the elasmobranch? 6) How host specific is the parasite? 7) What is the geographic distribution of the parasite? and 8) How much time does the parasite spend in the elasmobranch host, i.e., what is the duration of infection?

As will be seen below, the answers to some of these questions, such as whether a parasite is ectoparasitic or endoparasitic, can usually be generalized for any particular parasite group at the order or class level. However, the answers to other questions, such as distribution and host specificity, may differ significantly between congeneric parasite species. If information on all eight questions about the biology of a particular parasite species is not available, it merely limits the usefulness of the parasite as a biological indicator. In many instances partial parasite data may still be used to generate information on a subset of the six aspects of elasmobranch biology discussed below. For example, if the life history of a particular parasite species is not known, its use with respect to inferences about the feeding biology of its host is limited, but it can still be included in an analysis for inferring the phylogeny of its host.

Metazoan Parasites of Elasmobranchs

Reviews or summaries are currently available for several groups of elasmobranch parasites. For example, Benz (in press) discussed the copepod parasites of sharks, and Moreira and Sadowsky (1978) dealt with the isopod parasites of Chondrichthyes. In his paper discussing parasitism in the deep sea, Campbell (1983) provided an excellent summary of a number of aspects of the parasites of chondrichthyan fishes, and the histopathology associated with elasmobranch parasites was reviewed by Campbell (in press). To my knowledge, however, no comprehensive survey of the metazoan parasites of elasmobranchs exists.

Owing to time and space limitations, I will not present a comprehensive list of all parasite species ever recorded from an elasmobranch, rather I have confined myself to a discussion of each of the higher parasite taxa that are known to possess members that have been reported from elasmobranchs. I have included all groups regardless of whether hundreds of species in the group have been reported as elasmobranch parasites, for example the subclass Eucestoda, or only a single species in the group has been reported from elasmobranchs, for example the subclass Cirripedia. Investigators interested in the parasites associated with a particular elasmobranch species are referred to Part 7 (host index) of the Index-Catalogue of Medical and Veterinary Zoology (U.S. Dept. Agriculture).

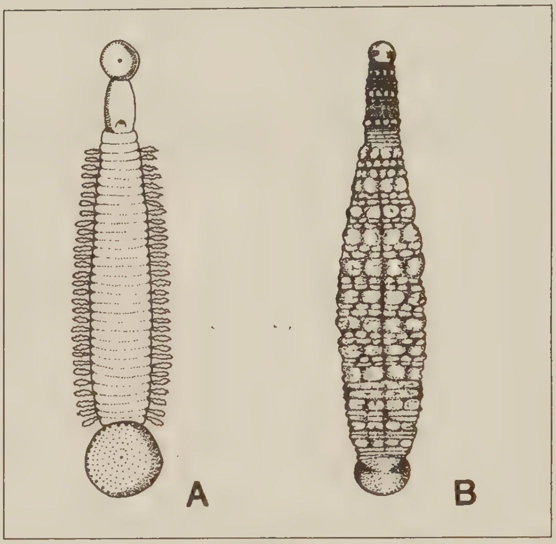

Figure 1.
Representatives of subfamilies of piscicolid leeches parasitic on elasmobranchs. A. Branchinellinae—*Branchellion ravenellii* (Girard 1850), ventral view. B. Ichthyobdellinae—*Stibarobdella macrothela* (Schmarda 1861), dorsal view. Both redrawn from Sawyer et al. (1975).

Of the 20 metazoan phyla that are known to possess parasitic members, only four have representatives that are frequently reported from elasmobranchs. These include the following phyla: Annelida, Nematoda, Platyhelminthes, and Arthropoda. On very rare occasions members of two additional phyla, the Acanthocephala and the Mollusca, have been reported as parasites of elasmobranchs. Each of these six groups is discussed separately below with emphasis on the four more frequently encountered phyla.

Phylum Annelida

Of the three currently recognized classes of Annelids, only the leeches (class Hirudinea) possess members that parasitize elasmobranchs. These species appear to be restricted to the family Piscicolidae Johnston 1865, a group of monoxenous ectoparasites. Not all species of piscicolids are elasmobranch parasites. Representatives of the Branchinellinae and the Ichthyobdellinae, the two subfamilies of piscicolids known from elasmobranchs, are illustrated in Figure 1.

The typical piscicolid life cycle (Fig. 2) involves only a single host on which the adult is found. The adult leech lays a cocoon containing a small number of eggs either directly on the elasmobranch or on the substrate. The juvenile leech hatches from the cocoon and attaches to the elasmobranch. Most piscicolids seem to prefer the marine environment, but a few have been reported from hosts in brackish waters. Piscicolid leeches have been found on a

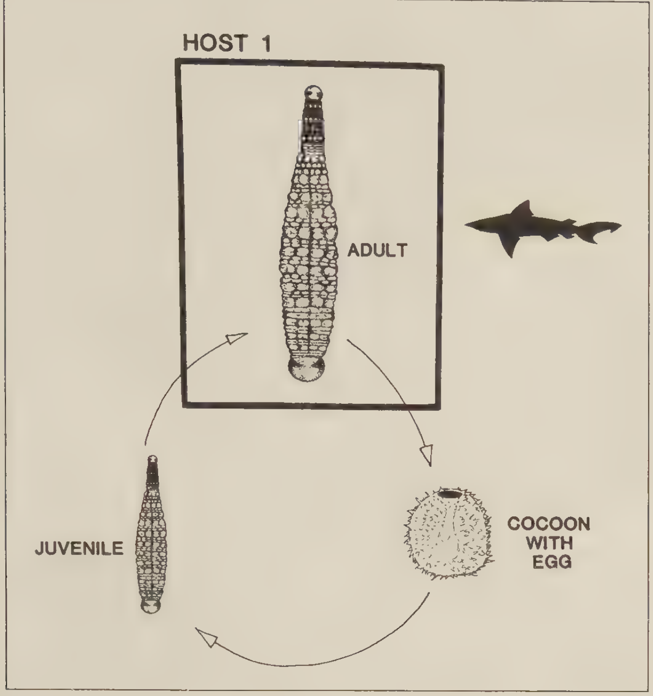

Figure 2.
Generalized leech life cycle showing involvement of elasmobranch host.

number of external sites on their elasmobranch hosts including the tail, between the eyes, on the tongue, and in the gill slits. These parasites do not appear to be extremely host specific. Several species have been reported to parasitize an extensive range of elasmobranch species as well as several teleost species (Sawyer et al. 1975).

Phylum Nematoda

Of the six currently recognized orders of nematode parasites of vertebrates (Willmott and Chabaud 1974), one in the subclass Adenophorea, the Enoplida, and three in the subclass Secernentea including the Ascaridida, Spirurida, and Strongylida possess members recorded as parasites of elasmobranchs. However none of these orders is exclusively parasitic in elasmobranchs. One family in the order Enoplida, the Trichuridae, has been reported from elasmobranchs. Records of this group consist of adult worms in some cases (Read 1948) and solely of eggs in others (MacCallum 1925). Three families of ascarids including the Anisakidae (Railliet and Henry 1912), the Acanthocheilidae Wülker 1929, and the Kathlaniidae (Lane 1914) possess species reported as parasites of elasmobranchs (Hartwich 1974). Baker (1987) suggested that the kathlaniid records may be cases of accidental parasitism. The acanthocheilids are currently known only from elasmobranchs. Five families of spirurids, including the Physalopteridae (Railliet 1893), Cystidicolidae (Skrjabin 1946), Philometridae Baylis and Daubny 1926, Cucullanidae Cobbold 1864 and the Gnathostomatidae Railliet 1895 (Chabaud 1975a, b, 1978) are known from elasmobranchs, but none of these families consists exclusively of elasmobranch parasites. A representative of the family Trichostrongylidae in the order Strongylida has been reported from an elasmobranch (Mawson 1954). As these worms were described from museum specimens of dubious host origin, the record is a tentative one. Representatives of these eight nematode families are illustrated in Figure 3.

The life cycles of elasmobranch nematodes are poorly known, thus generalization is difficult. It appears that some species are monoxenous whereas others have life cycles involving at least two different host species. A two-host life cycle is illustrated in Figure 4. The elasmobranch appears to play the role of intermediate host for some nematodes, for example, larval philometrids have been found in elasmobranchs (Benz et al. 1987). Elasmobranchs are also known to play the role of definitive host, for example, adults of *Acanthocheilus quadridentatus* Molin 1858 have been reported from a number of elasmobranch species (Diaz 1972). Nematodes of elasmobranchs, whether parasitic as larvae or adults, are generally internal parasites. The sites of larval nematodes range from the uterus (Benz et al. 1987) and ovaries (Rosa-Molinar et al. 1983) to superficial body tissues (de Ruyck and Chabaud 1960). Adult nematodes have been reported from the stomach (Diaz 1972), spiral valve (McVicar 1977), and pancreatic duct (McVicar and Gibson 1975) as well as from ulcer-like lesions in the external surfaces of their elasmobranch hosts (Adamson et al. 1987).

Phylum Platyhelminthes

Four classes of platyhelminths contain species reported as parasites of elasmobranchs: 1) the Trematoda, among which two subclasses the Aspidocotylea and the Digenea are represented, 2) the Monogenea, 3) the Turbellaria, and 4) the Cestoidea, of which only the subclass Eucestoda is represented in elasmobranchs. Because of the tremendous differences in morphology and biology between these groups each is discussed separately below.

Class Trematoda

Subclass Aspidocotylea—Species belonging to two families of aspidocotyleans, the Stichocotylidae Faust and Tang 1936, and Aspidogasteridae Poche 1907, have been reported from elasmobranchs. Examples of each are illustrated in Figure 5. The former is a monotypic group. The sole species, *Stichocotyle nephropis* Cunningham 1884, is parasitic as an adult in the bile ducts and gall bladder of rays (Schell 1985). In the latter group at least one species of *Multicalyx* (Faust and Tang 1936) is parasitic as an adult in the bile ducts and gall bladder of elasmobranchs (Thoney and Burreson 1987).

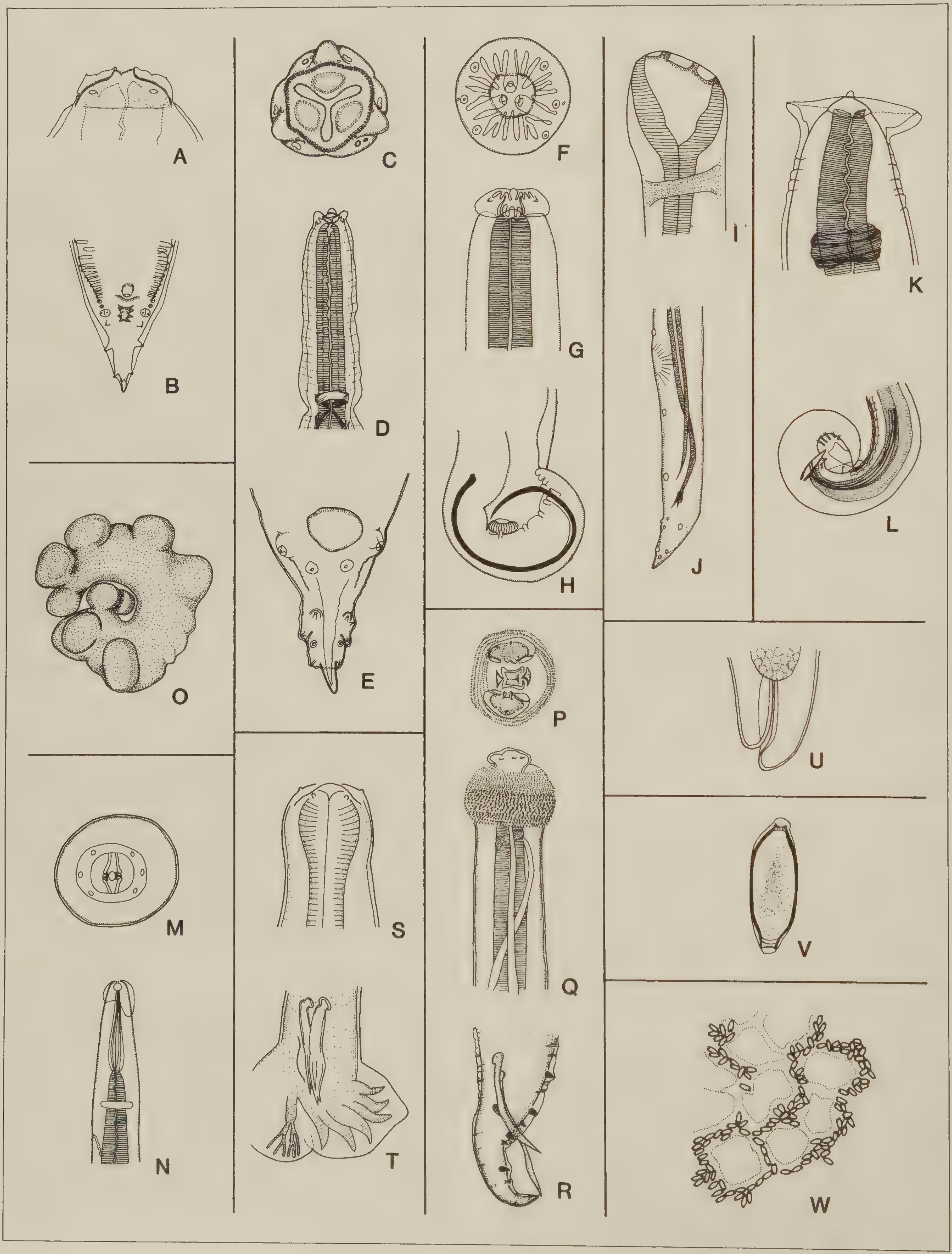
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Figure 3.

Representatives of families of Nematoda parasitic in elasmobranchs. a–h = order Ascaridida; i–r = order Spirurida; s, t = order Strongylida; u–w = order Enoplida. a–b = Anisakidae—*Terranova ginglymostomae* Olsen 1952, a—anterior extremity dorsal view, b—posterior extremity of male ventral view, spicule omitted (a and b redrawn from Olsen 1952). c–e = Acanthocheilidae—*Pseudanisakis rotundata* (Rud. 1819), c—anterior extremity apical view, d—anterior extremity lateral view, e—posterior extremity of male ventral view (c and d redrawn from Williams and Richards 1968; e redrawn from Yamaguti 1961). f–h = Kathlaniidae—*Tonaudia chiloscylii* (Thwaite 1927), f—anterior extremity apical view, g—anterior extremity lateral view, h—posterior extremity of male lateral view (f and g redrawn from Inglis 1957). i–j = Cucullanidae—*Cucullanus heterodonti* Johnston and Mawson 1943, i—anterior extremity lateral view, j—posterior extremity of male lateral view (i and j redrawn from Johnston and Mawson 1943). k, l = Physalopteridae—*Proleptus obtusus* Duj. 1845, k—anterior extremity lateral view, l—posterior extremity of male lateral view (k and l redrawn from Yorke and Maplestone 1926). m, n = Cystidicolidae—*Parascarophis sphyrnae* Campana-Rouget 1955, m—anterior extremity apical view, n—anterior extremity lateral view (m and n redrawn from Yamaguti 1961). o = Philometridae—*Phlyctainophora lamnae* Steiner 1921, o—lateral view of adult female (redrawn from Yorke and Maplestone 1926). p–r = Gnathostomatidae—*Echinocephalus overstreeti* Deardorff and Ko 1983, p—anterior extremity apical view, q—anterior extremity lateral view, r—posterior extremity of male lateral view (all redrawn from Deardorff and Ko 1983). s, t = Trichostrongylidae—*Ichthyostrongylus clelandi* Mawson 1954, s—anterior extremity lateral view, t—posterior extremity of male ventral view (s and t redrawn from Mawson 1954). u–w = Trichuridae—*Capillaria hathawayi* Read 1948, u—posterior extremity of female, v—egg (both redrawn from Read 1948), w—*Capillaria carcharhini* MacCallum 1925, portion of skin of shark with eggs of the parasite between dentacles (redrawn from MacCallum 1925).

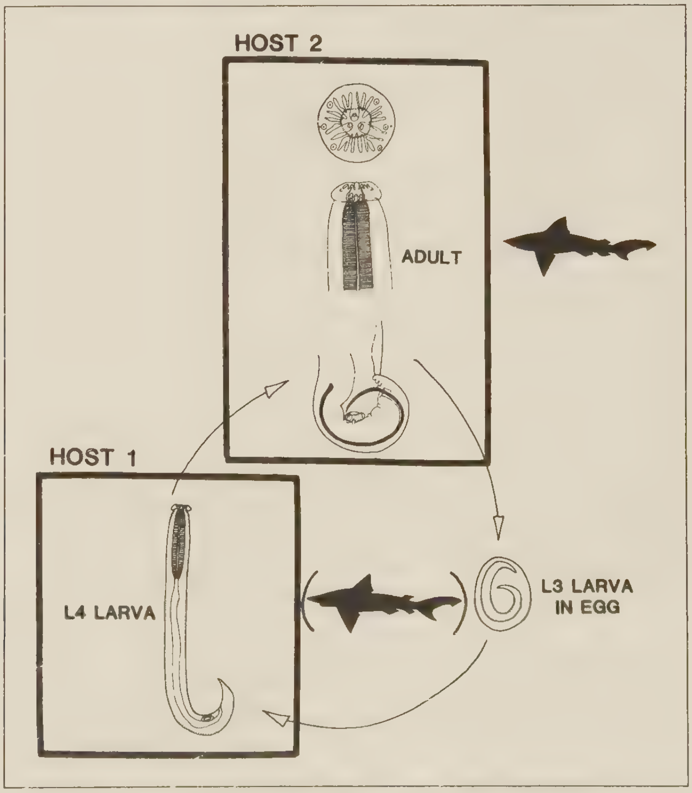

Figure 4.

Possible generalized two-host nematode life cycle illustrating involvement of elasmobranchs as hosts. Parentheses around elasmobranch silouette indicate larvae are infrequently found in elasmobranchs. (Note: the second to last and the last larval stage in the nematode life cycle are referred to as the L3 and L4 larva, respectively.)

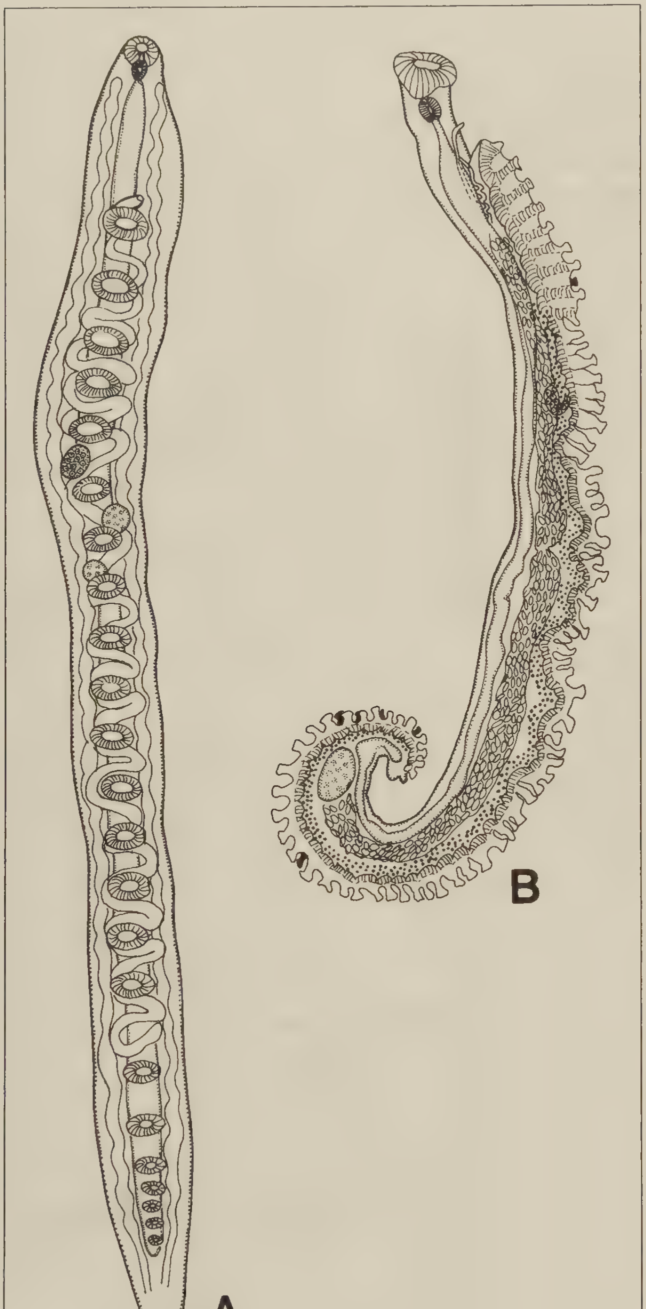

Figure 5.
Representatives of families of Aspidocotylea parasitic in elasmobranchs. A. Stichocotylidae—*Stichocotyle nephropis* Cunningham 1884, ventral view, modified from Schell (1985). B. Aspidogasteridae—*Multicalyx cristata* (Faust and Tang 1936), lateral view, modified from Manter (1954).

The typical aspidocotylean life cycle involves a free-swimming larval form, or cotylocidium, and perhaps two hosts (Fig. 6). The adult worm lays eggs that pass to the outside via the digestive system of the host and then hatch to release the free-swimming cotylocidium. These larvae search for the intermediate host, enter, and encyst. Here they develop into preadults. Preadults of *S. nephropis* have been found encysted in the rectum of lobsters (Schell 1985). When the intermediate host is eaten by the elasmobranch, the preadults escape from the cyst, travel to the bile ducts, and develop into adults. Thoney and Burreson (1986) presented evidence which suggested that after establishment in the first intermediate host *Multicalyx cristata* may enter a teleost host in which no development of the parasite occurs, but which serves to bridge a food chain gap, thus facilitating transfer to the elasmobranch final host.

Subclass Digenea—Of the 71 recognized families of Digenea parasitizing vertebrates (Yamaguti 1971), seven possess members known to parasitize elasmobranchs. Representatives of each of these groups are illustrated in Figure 7. Sites of preference within the elasmobranch reported by Yamaguti (1971) for each family are as follows: The Azygiidae Odhner 1911, Aphanhysteridae Yamaguti 1958, and Ptychogonimidae Dollfus 1937 have been reported from the digestive tract; the Gorgoderidae Looss 1901 are known from various regions of the body cavity; the Syncoeliidae (Looss 1899) have been reported from the branchial cavity and skin; the Didymozoidae Poche 1907 from the walls of the gill chambers; and the Sanguinicolidae Graff 1907 have been reported from the various blood vessels associated with the heart. Only the Aphanhysteridae appear to be restricted in distribution to elasmobranchs.

Unfortunately, complete life-history data are not available for a single species of digenean that parasitizes elasmobranchs. Based on the life histories of digeneans from other fishes (for example Schmidt and Roberts 1985), the following life cycle is probable. A free-swimming miracidium hatches from the egg, finds the first host, which is a mollusc of some kind, develops into a sporocyst and/or then a redia that in turn produces a number of free-swimming cercariae. The cercariae encyst in or on a second intermediate host and develop into metacercariae. When this host is eaten by the elasmobranch, the adult form develops. This life-history scenario is summarized in Figure 8. The adult is the only digenean stage that has been reported from elasmobranchs, thus elasmobranchs appear to serve only as definitive hosts for these parasites.

Class Monogenea—Both orders of Monogenea possess species reported as parasites of elasmobranchs (Fig. 9) (Yamaguti 1963a). In the order Polyopisthocotylea, the Hexabothriidae Price 1942 is the only family known from elasmobranchs, and the group appears to be restricted in distribution to these fishes. Seven families in the order Monopisthocotylea have been recorded from elasmobranchs including the Dactylogyridae Bychowsky 1933, Capsallidae Baird 1853, Monocotylidae Taschenberg 1878, Udonellidae Taschenberg 1879, Acanthocotylidae Price 1936, Loimoidae Bychowsky 1957, and Microbothriidae Price

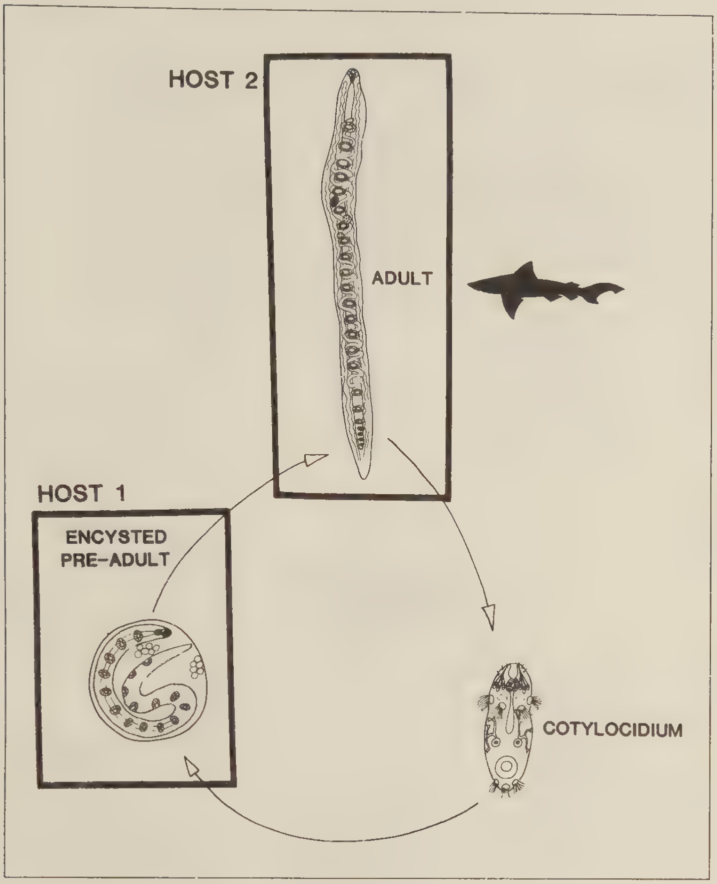

Figure 6.
Possible generalized aspidocotylean life cycle involving elasmobranch host.

1936. The latter three families appear to be restricted in host distribution to elasmobranchs. Many of the udonellids are actually hyperparasites of copepods that parasitize elasmobranchs. With the exception of some of the Monocotylidae, the remaining monogeneans are ectoparasites associated with various regions of the skin, mouth, branchial chamber, or rectum of their elasmobranch hosts. A number of species of Monocotylidae are unusual for monogeneans in that, rather than being ectoparasitic, they are endoparasitic within the coelom, rectal gland, or oviducts of their hosts (Yamaguti 1963a).

The typical monogenean life cycle (Fig. 10) is relatively simple, involving only a single host. The adult worm lays eggs that either float freely in the water column or occasionally are attached to a substrate. A ciliated free-swimming oncomiracidium hatches from the egg, searches for the host, and matures into the adult form. Only adult Monogenea are known from elasmobranchs.

Class Cestoidea

Subclass Eucestoda—Of the 13 orders of tapeworms recognized in the subclass Eucestoda (Schmidt 1986), six have members known to parasitize elasmobranchs. These include the Tetraphyllidea, Trypanorhyncha, Lecanicephalidea, Diphyllidea, Litobothridea, and Dioecotaeniidea. Representatives of each of these orders are illustrated in Figure 11. The eucestodes are somewhat unusual in that, as adults, all of the species in all six of the above orders are exclusively parasitic in elasmobranchs. Thus, tapeworms are not only one of the most diverse groups of elasmobranch parasites, but also one of the most frequently encountered.

In general, the life histories of elasmobranch tapeworms are very poorly known. These data are available for only a few species (for example, Overstreet 1978). It appears that the successful completion of a life cycle may involve anywhere from two to perhaps five hosts, depending on the parasite species. A generalized life cycle is illustrated in Figure 12. The adult tapeworm releases eggs, from which free-swimming coracidium larvae hatch. These larvae are eaten by the first intermediate host, often copepods, in which the coracidium develops into the second larval form called a procercoid. When this first host is eaten by the second host, often a teleost or mollusc, the tapeworm develops further into the third larval form called a plerocercoid. When this second intermediate host is consumed by the third host, often an elasmobranch, the tapeworm matures into the adult form. In most instances elasmobranchs are parasitized by adult tapeworms and therefore play the role of definitive host. The plerocercoids of a number of tapeworm species have been found in elasmobranchs, thus elasmobranchs may also play the role of

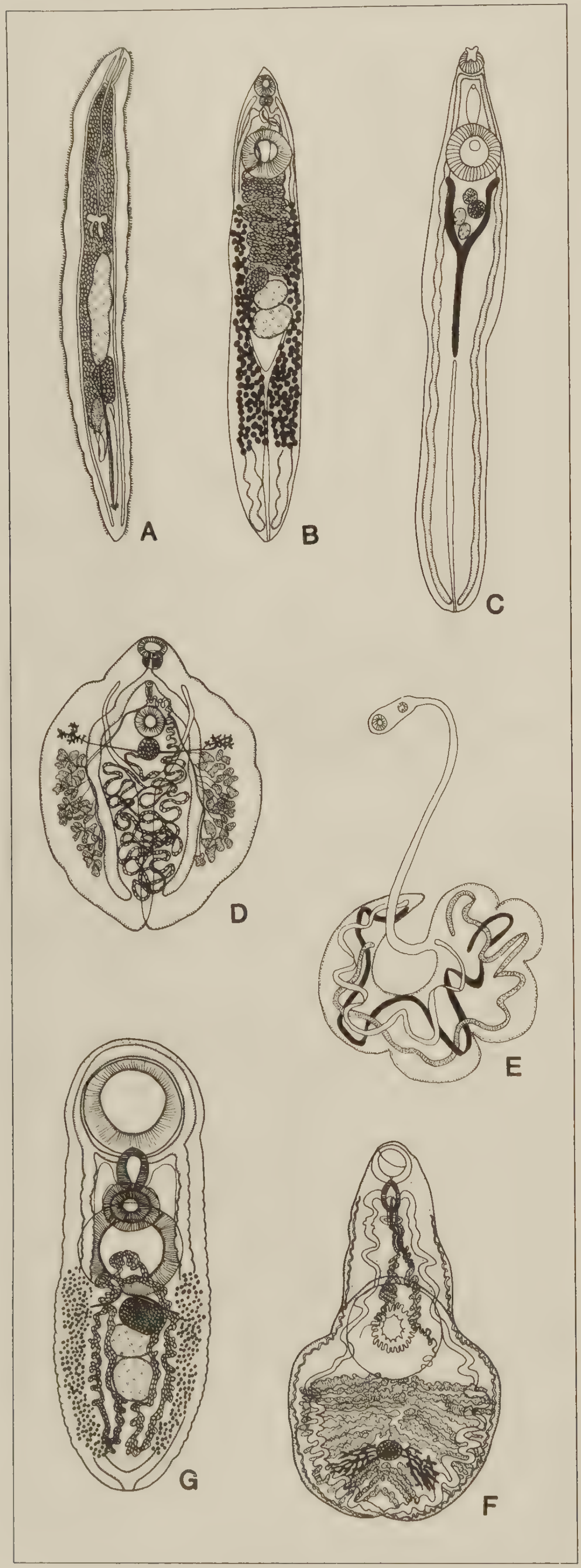

Figure 7.
Representatives of families of Digenea parasitic in elasmobranchs. A. Sanguinicolidae—*Selachohemecus olsoni* Short 1954. B. Azygiidae—*Otodistomum veliporum* (Creplin 1837). C. Aphanhysteridae—*Aphanhystera monacensis* Guiart 1938. D. Gorgoderidae—*Probolitrema richardii* (Lopez 1888). E. Didymozoidae—*Tricharrhen okenii* (Koelliker 1847). F. Syncoeliidae—*Paronatrema vaginicola* Dollfus 1937. G. Ptychogonimidae—*Ptychogonimus megastomus* (Rud. 1819). C, E, modified from Yamaguti (1971); A, B, D, F, G, redrawn from Yamaguti (1971); A–F ventral views, G dorsal view.

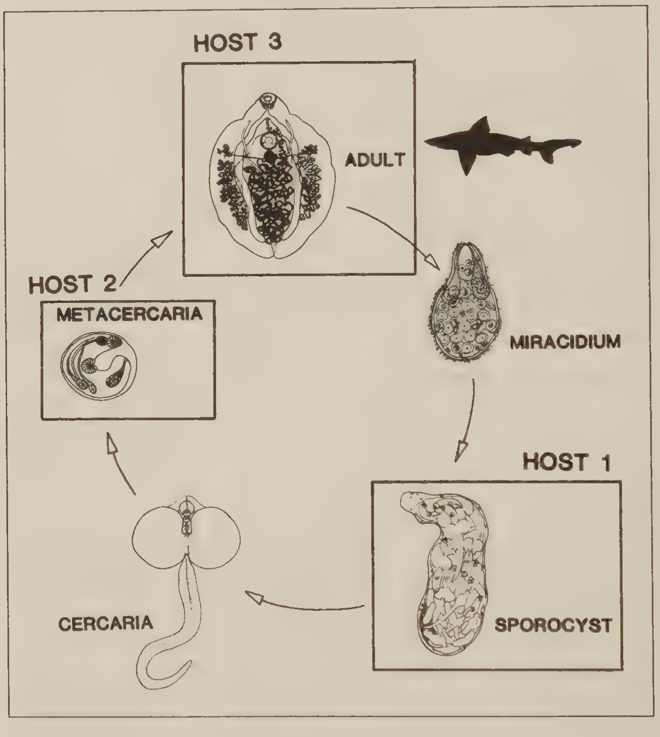

Figure 8.
Possible generalized digenean life cycle involving elasmobranch host.

intermediate host. Adult tapeworms are usually found associated with the spiral valve. Plerocercoids inhabit a broader range of sites including the liver, body cavity, and mesentaries.

Class Turbellaria—Although the majority of the turbellarians are free-living, adults of a single species, *Micropharynx parasitica* (Jägerskiöld 1896), have been reported as parasites of elasmobranchs (see Fig. 15) (Ball and Khan 1976). Little is known about the life history of *M. parasitica*. Ball and Khan (1976) suggested that this species is similar to other marine planarians because a pelagic stage is lacking from the life cycle. Transfer of worms from host to host may occur during the copulation of elasmobranchs.

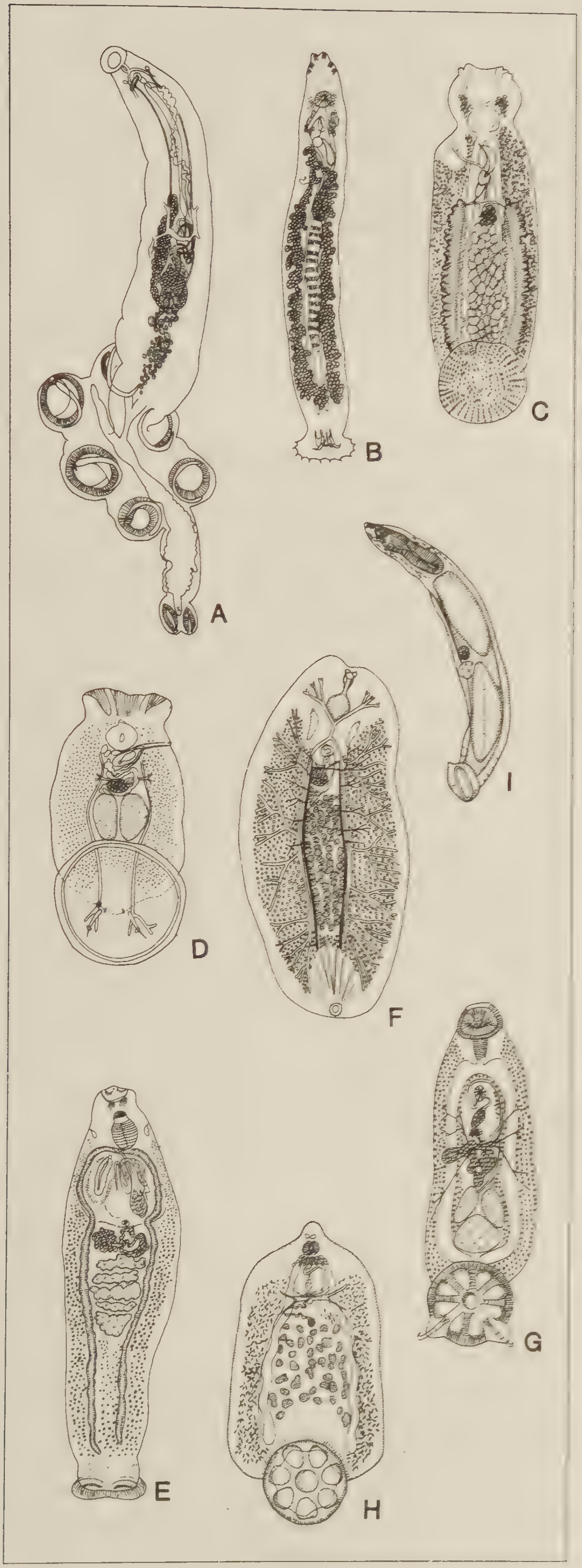

Figure 9.
Representatives of families of Monogenea parasitic on elasmobranchs. A. Hexabothriidae—*Erpocotyle catenulata* Guberlet 1933. B. Dactylogyridae—*Amphibdelloides maccallumi* (Johnston and Tiegs 1922). C. Acanthocotylidae—*Pseudacanthocotyla pacifica* (Bonham and Guberlet 1938). D. Capsallidae—*Pseudoentobdella pacifica* (Guberlet 1936). E. Loimoidae—*Loimos scoliodoni* (Manter 1938). F. Microbothriidae—*Pseudocotyle squatinae* van Beneden and Hesse 1865. G. Monocotylidae—ectoparasite, *Monocotyle myliobatis* Taschenberg 1878. H. Monocotylidae—endoparasite, *Gymnocalicotyle inermis* (Woolcock 1936). I. Udonellidae—*Calinella craneola* Monticelli 1910. A–I, redrawn from Yamaguti (1963a); A–D and F–I ventral views; E, dorsal view.

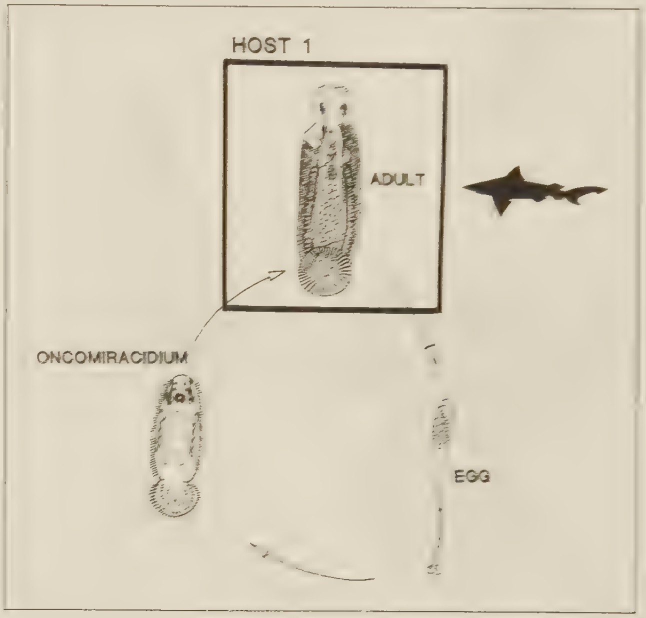

Figure 10.
Generalized monognean life cycle involving elasmobranch host.

Phylum Arthropoda

The arthropod parasites of elasmobranchs are restricted to three classes within the subphylum Crustacea. These include 1) three subclasses within the class Maxillopoda: the Copepoda, the Cirripedia, and the Branchiura; 2) the class Malacostraca including two orders in the subclass Eumalacostraca, the Isopoda and the Amphipoda; and 3) the class Ostracoda. Because of the diverse morphology and biology of the various crustacean subgroups, each will be discussed separately below following the classification scheme of Bowman and Abele (1982).

Class Maxillipoda

Subclass Copepoda—Members of two of the eight orders of copepods have been reported as parasites of

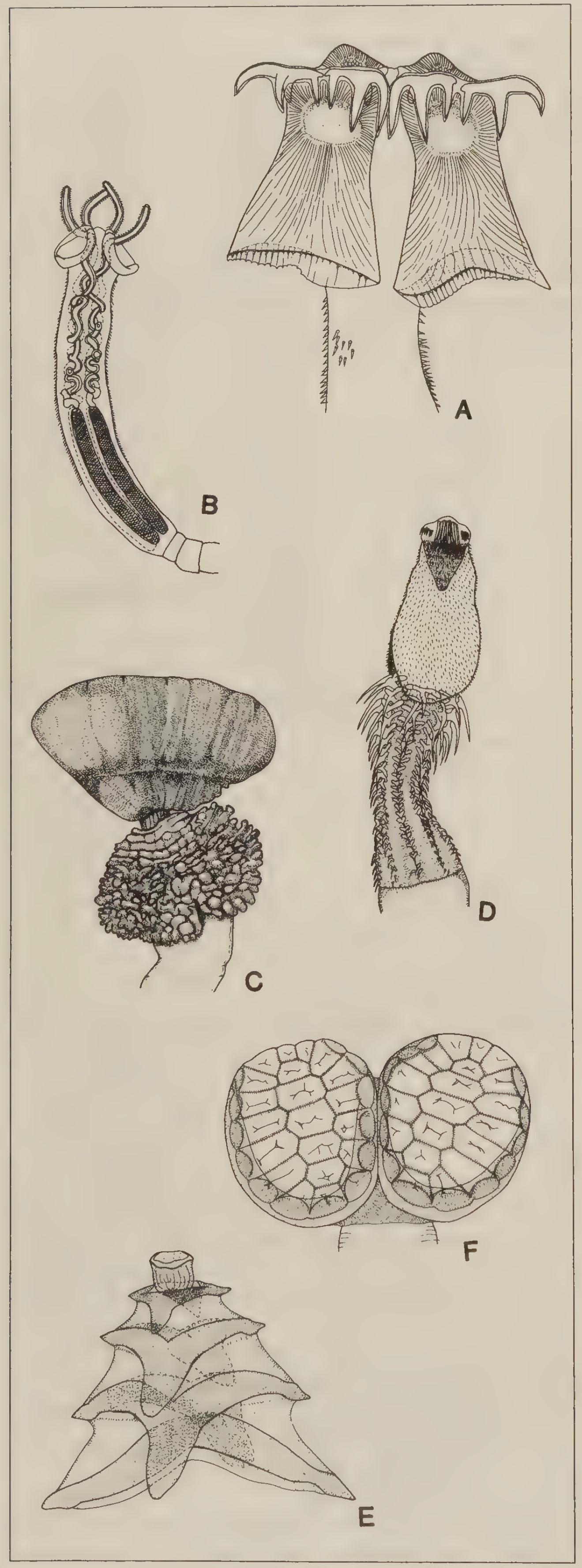

Figure 11.
Representatives of orders of Eucestoda parasitic in elasmobranchs. A. Tetraphyllidea—*Phoreiobothrium lasium* Linton 1889, from Caira (1985). B. Trypanorhyncha—*Mecistobothrium brevispine* (Linton, 1897), redrawn from Campbell and Carvajal (1975). C. Lecanicephalidea—*Disculiceps galapagoensis* Nock and Caira 1988, from Nock and Caira (1988) D. Diphyllidea—*Echinobothrium bonasum* Williams and Campbell 1980, redrawn from Williams and Campbell (1980). E. Litobothridea—*Litobothrium coniformis* Dailey 1969, redrawn from Dailey (1969). F. Dioecotaeniidea—*Dioecotaenia cancellata* (Linton 1890), redrawn from Schmidt (1969). A–F dorsal or ventral views of scolices.

elasmobranchs. These orders include the Poecilostomatoida and the Siphonostomatoida. Within the former order only two families, the Taeniacanthidae Wilson 1911, and the Chondracanthidae Milne-Edwards 1840, include species that parasitize elasmobranchs, but neither is restricted in distribution to this host group. Representatives of 11 of the 44 families of siphonostome copepods have been reported from elasmobranchs (Kabata 1979). These include the Pandaridae Milne-Edwards 1840, Sphyriidae Wilson 1919, Caligidae Burmeister 1835, Dichelesthiidae Dana 1853, Eudactylinidae Yamaguti 1963, Lernaeopodidae Olsson 1869, Dissonidae Yamaguti 1963, Trebiidae Wilson 1932, Euyphoridae Wilson 1905, Kroyeriidae Kabata 1979, and Cecropidae Dana 1852. Representatives of each family are illustrated in Figure 13. Only the Kroyeriidae is restricted in distribution to elasmobranchs. All members of both orders that parasitize elasmobranchs are essentially ectoparasitic. Attachment sites range from the fins, claspers, and nares to the buccal and branchial regions of the host. The copepod parasites of elasmobranchs are second only to the tapeworms with respect to their abundance and species diversity.

The life histories of elasmobranch copepods are poorly known. A probable life cycle is illustrated in Figure 14. In general, copepods of elasmobranchs pass through only one or two naupliar stages both of which are free-swimming in nature (Benz, in press). The nauplius molts to the copepodid stage and finds the elasmobranch host. The copepodid may molt to a filamented chalimus stage, which subsequently molts to the preadult stage. The preadult usually molts two additional times until it ultimately develops into the adult.

Subclass Cirripedia—A single species of parasitic barnacle, *Anelasma squalicola* Loven, has been reported from elasmobranchs. Adults of this species have been found partially embedded (Fig. 16) near the dorsal spine or around the pectoral and pelvic fins of their hosts. This species develops from a free-living nauplius stage to a free-living cypris stage, which is infective and matures into the adult form on elasmobranchs (Kabata 1970).

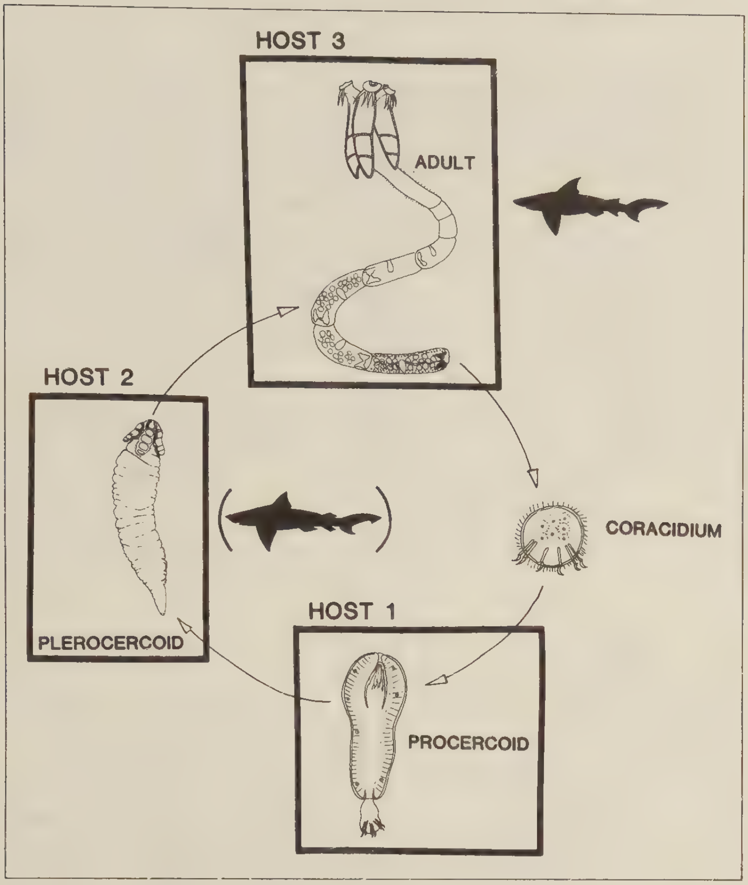

Figure 12.
Generalized three-host cestode life cycle illustrating involvement of elasmobranchs as hosts. Parentheses indicate plerocercoids are infrequently found in elasmobranchs. Plerocercoid redrawn from Cake (1976).

Subclass Branchiura—Of the four genera of branchiurans recognized by Cressey (1983), only a few of the 100 species in the genus *Argulus* Mueller 1785 (Fig. 17) have been reported to parasitize elasmobranchs (for example, Pearse 1953). Branchiurans deposit eggs on the bottom. Simnura (1981) described the development of a species of *Argulus* in detail. He found that a copepodid form hatches from the egg, finds a host and matures through nine larval stages separated by molts into the adult form. All species are ectoparasitic and appear to feed through the skin of their hosts.

Class Malacostraca

Order Isopoda—The isopod parasites of elasmobranchs can be divided into two groups: those parasitic as larvae, including some of the members of the family Gnathiidae Harger 1880 in the suborder Gnathiidea, and those parasitic as adults, including some of the members of the families Cirolanidae Dana 1853, Excorallanidae Stebbing 1904, Aegidae Leach 1815, and Cymothoidae Dana 1852, in the suborder Flabellifera (Moreira and Sadowsky 1978). Representatives of both suborders are illustrated in Figure 18. Both groups are ectoparasitic. Neither is restricted in distribution to elasmobranchs.

The life cycles of parasitic isopods are not well known. Some species may be polyxenous utilizing intermediate hosts (Overstreet 1978) In the Gnathiidea, newly hatched larvae pass through a brief swimming phase and metamorphose into the ''pranzia'' stage that attaches to the elasmobranch, usually on the gills, mouth, or skin and feeds on blood (Kabata 1970). This stage eventually leaves the host and matures into a free-swimming adult. In the Flabellifera, young forms attach to the elasmobranch, often in the region of the gills, and mature to the adult form. In some species of Cymothoidae, individuals attach to the gill chamber as males, and then transform into females and move to the mouth region (Schmidt and Roberts 1985).

Order Amphipoda—Only a small number of amphipods appear to be parasites of fishes, and only a very small subset of these parasitize elasmobranchs. For example, adults of *Laphysticus sturionis* Kroyer 1842 (Fig. 19) are ectoparasitic on protected regions, such as under the pectoral fins, of skates (Kabata 1970).

Class Ostracoda—Although ostracods are rarely parasitic, adults (Fig. 20) of several species have been reported to parasitize the gills and nostrils of elasmobranchs (Kabata 1984). Little is known about the life history of these parasitic species.

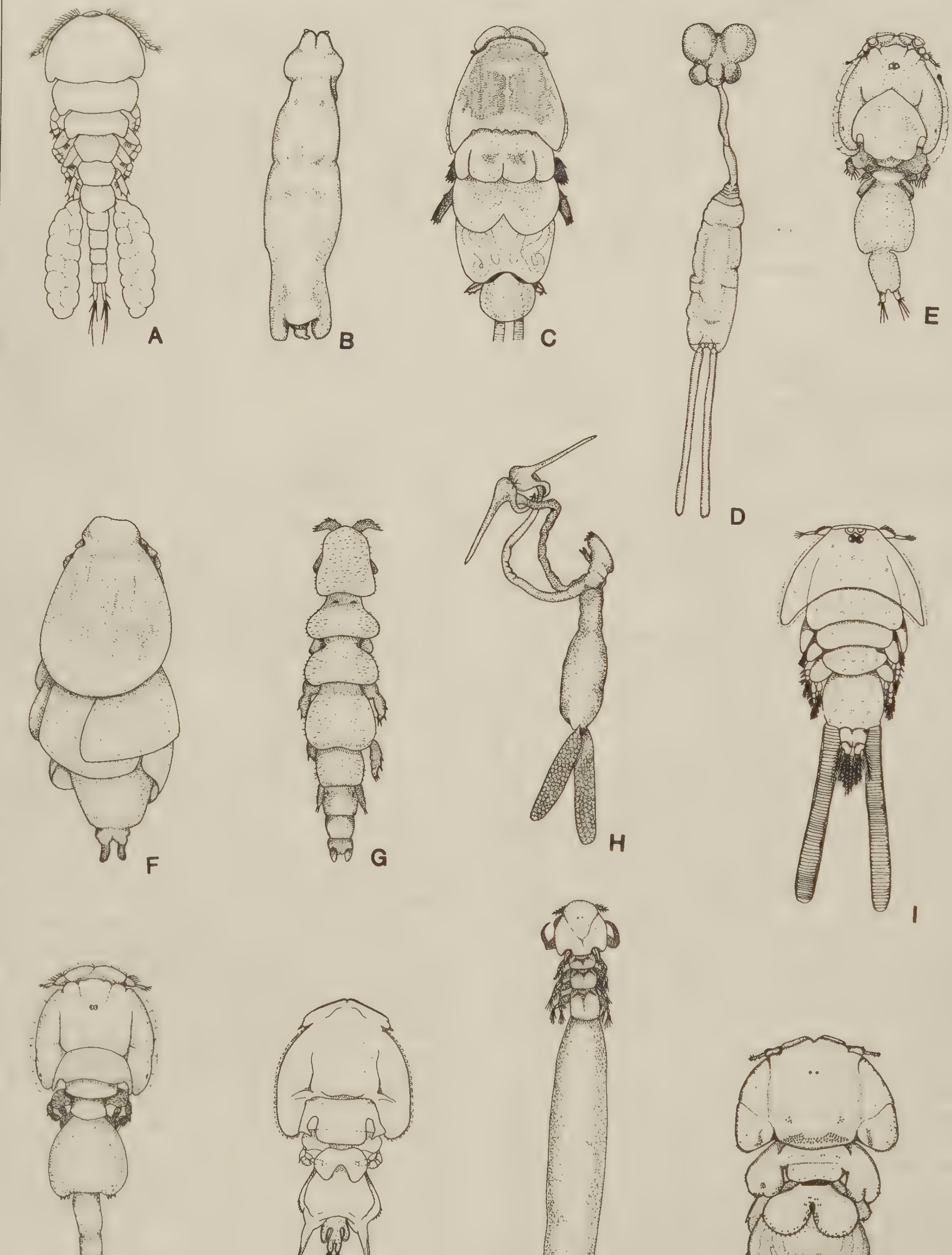
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Figure 13.
Representatives of families of Copepoda parasitic on elasmobranchs. A, B = order Poecilostomatoida, C–M = order Siphonostomatoida. A. Taeniacanthidae—*Taeniacanthus wilsoni* Scott 1929. B. Chondracanthidae—*Acanthochondrites annulatus* (Olsson 1869). C. Pandaridae—*Pandarus bicolor* Leach 1816. D. Sphyriidae—*Paeon vaissierei* Delamere-Deboutteville and Nunes-Ruivo 1953. E. Caligidae—*Caligus elongatus* Nordmann 1832. F. Dichelesthiidae—*Anthosoma crassum* (Abildgaard 1794). G. Eudactylinidae—*Eudactylina similis* Scott 1902. H. Lernaeopodidae—*Schistobrachia ramosa* (Kroyer 1863). I. Dissonidae—*Dissonus spinifer* Wilson 1906. J. Trebiidae—*Trebius caudatus* Kroyer 1838. K. Euryphoridae—*Alebion carchariae* Kroyer 1863. L. Kroyeriidae—*Kroyeria lineata* van Beneden 1853. M. Cecropidae—*Entepherus laminipes* Bere, 1936. A–G, I–M, dorsal views of females; H, lateral view of female; A–C, E–H, J, and L redrawn from Kataba (1979); D, redrawn from Lewis (1966); I, redrawn from Wilson (1907); K, redrawn from Cressey (1972); M, redrawn from Benz and Deets (1988).

Phylum Acanthocephala

Records of acanthocephalans from elasmobranchs are rare. It has been suggested by Williams et al. (1970) that this is the result of these organisms' inability to tolerate the high levels of urea in elasmobranchs. To date, all records of acanthocephalans from elasmobranchs are of adults (Fig. 21) from the spiral valves of their hosts. For example, Golvan et al. (1964) found adults of *Megapriapus ungriai* (Gracia-Rodrigo 1960) in the spiral valve of *Potamotrygon hystrix*. No information is currently available on the life histories of elasmobranch acanthocephalans. The species in other marine fishes generally develop into three larval stages, the acanthor, acanthella, and cysticanth, prior to the adult. Most require one or two host species prior to the fish host. Owing to the infrequency with which acanthocephalans parasitize elasmobranchs (I know of only seven records) they are of limited use as biological indicators and will not be discussed further. Individuals interested in reading about this group in more depth are referred to Crompton and Nickol (1985).

Phylum Mollusca

To my knowledge there exists a single record of a member of the phylum Mollusca parasitic on an elasmobranch. O'Sullivan et al. (1987) reported the snail *Cancellaria cooperi* Gabb (the cooper's nutmeg) (Fig. 22) from the dorsal surface of *Torpedo californica* Ayres. As this is the sole record of this phyllum from elasmobranchs, the phylum will not be considered further.

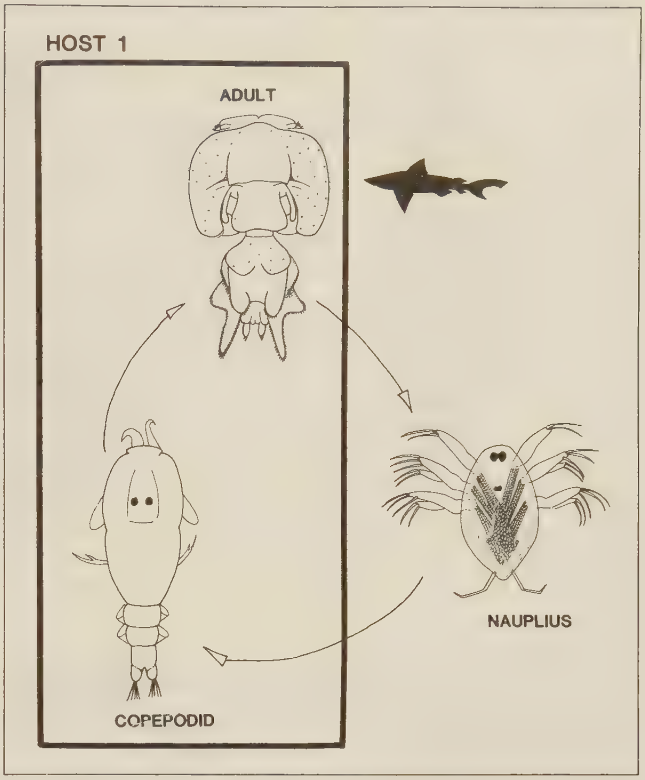


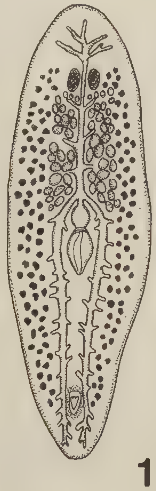
Figure 14.
Generalized one-host copepod life cycle involving elasmobranch host. Nauplius, copepodid, and adult redrawn from Benz (in press).

Metazoan Parasites as Biological Indicators for Elasmobranchs

1. Geographic Movements and Migrations

Kabata (1963) listed five conditions regarding the use of parasites as biological tags for monitoring the movements of marine fishes. These conditions are 1) Among populations of the host species, the parasite should be common in one population and rare or absent in another; 2) It is preferable that the life cycle of the parasite include only the host species that is the object of the study, i.e., the parasite should be monoxenous and host specific; 3) Infections with the parasite should be of reasonably long duration; 4) The incidence of the parasite must remain relatively stable, both within an annual cycle and from year to year; 5) Environmental conditions throughout the area studied should be within the physiological range of the parasite intended as a tag.

Not all of these conditions need be met in order for a parasite to be useful as a tag. In many cases parasites that have single-host life cycles, for example some isopods, also have relatively short associations with their hosts. On the



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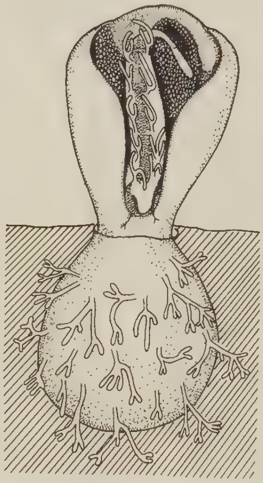

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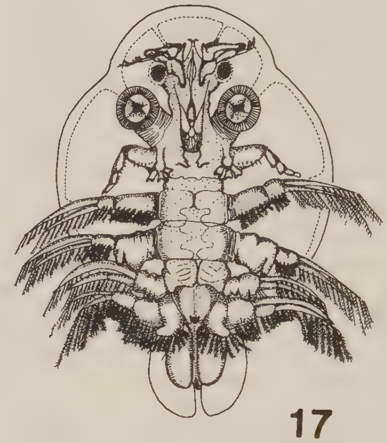

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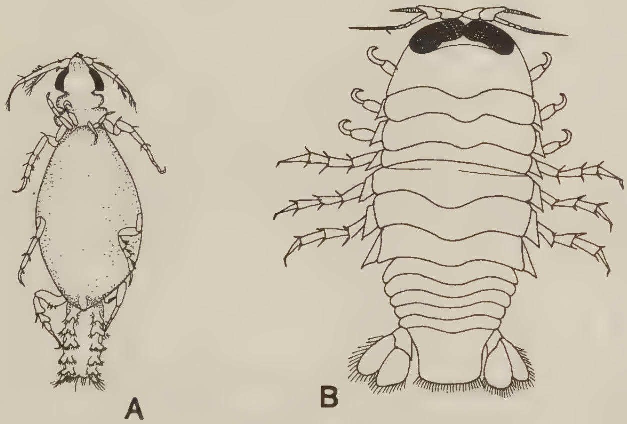

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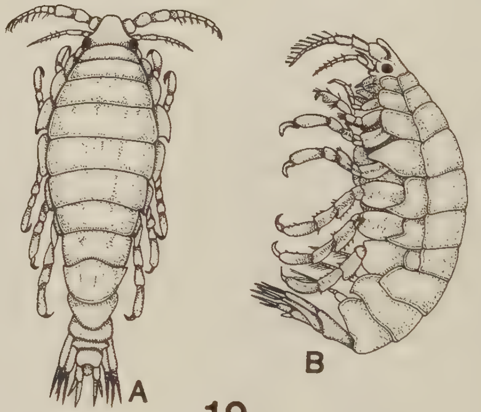

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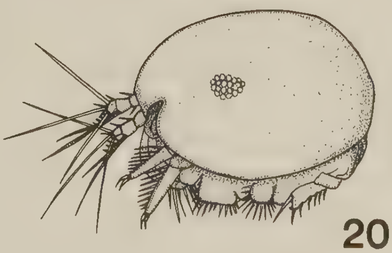

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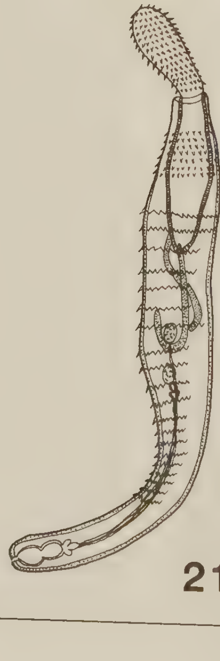

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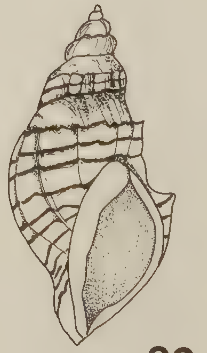

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Figure 15–22.
Minor groups parasitic on elasmobranchs.

Figure 15—Ectoparasitic turbellarian, *Micropharynx parasitica* (Jägerskiöld 1896), from elasmobranch; dorsal view; redrawn from Ball and Khan (1976).

Figure 16—Species from subclass Cirripedia parasitic on elasmobranchs—*Anelasma squalicola*, adult embedded in host tissue, redrawn from Baer (1951).

Figure 17—A representative species from subclass Branchiura parasitic on elasmobralıcns—*Argulus laticauda* Smith 1872, ventral view, redrawn from Wilson (1903).

Figure 18—Representatives of suborders of Isopoda parasitic on elasmobranchs. A. Suborder Gnathiidea—*Gnathia* sp. pranzia larva, ventral view, redrawn from Kabata (1970). B. Suborder Flabellifera—*Aega crenulata* (Lutken), adult, dorsal view, redrawn from Schultz (1969).

Figure 19—A representative species from order Amphipoda parasitic on elasmobranchs—*Laphystius sturionis* Kroyer 1842: A. dorsal view, B. lateral view, both redrawn from Kabata (1970).

Figure 20—Representative of class Ostracoda parasitic on elasmobranchs—*Cipridina parasitica* (Wilson 1913), lateral view of male, redrawn from Wilson (1913).

Figure 21—A representative species from phylum Acanthocephala parasitic in elasmobranchs—*Serrasentis longus* Tripathi 1959, males, redrawn from Yamaguti (1963b).

Figure 22—The only species of the phylum Mollusca currently known from elasmobranchs—*Cancellaria cooperi* Gabb, redrawn from Morris (1966).

other hand, many of the host-specific internal parasites, such as the tapeworms, are associated with their hosts for extended periods of time, but possess two or more hosts in their life cycles. These short host associations and polyxenous life cycles invoke additional considerations, but they do not preclude these parasites from use. Members of any of the four major phyla of elasmobranch parasites can supply information about elasmobranch migrations, but, each of the above conditions should be taken into consideration when determining the suitability of any particular parasite species for this purpose.

Example: For some time the possibility of marine migrations of *Carcharhinus leucas* (Valenciennes 1839) and *Pristis perotteti* Müller and Henle 1841 between Lake Nicaragua and the Caribbean Sea via the Rio San Juan has been a topic of discussion. Marine migrations of the bull shark were finally confirmed by Thorson (1971) after the recovery of sharks in Lake Nicaragua that had been tagged on the east coast of Costa Rica. Although this phenomenon was established with tagging, Watson and Thorson (1976) examined the parasite fauna in this system and provided parasite evidence sufficient to confirm the migrations in both the bull shark and the sawfish. Between the two species of elasmobranchs they discovered five species of monogeneans and 14 species of cestodes. Their results provide the following four pieces of evidence that support the marine migrations of both elasmobranch species: 1) Ten of the 11 species of monogeneans and tapeworms found, which were not new to science, have been reported previously from marine environments only; 2) All other known species in the three genera to which the seven newly described species belong have been reported previously from marine environments only; 3) One hundred and seventy-nine freshwater teleosts, representing seven families, examined from Lake Nicaragua did not harbour larvae of the tapeworms found as adults in the elasmobranchs. This strongly implicates marine teleosts as the source of the tapeworm infections in the elasmobranchs; 4) Overall, the abundance of parasites dropped, and the condition of remaining parasites degenerated, in hosts collected farther and farther upstream from the Caribbean Sea.

2. Feeding Biology

Parasites that are informative as indicators of the feeding biology of their hosts should satisfy the following conditions: 1) They must be polyxenous, requiring more than the elasmobranch host species within their life cycles; 2) The larval form found in the host that precedes the elasmobranch must be taxonomically identifiable. In general, the more exact the identification of the larval form, the greater the amount of information that can be obtained from it; 3) The larval parasite must exhibit specificity for the host that precedes the elasmobranch in its life cycle. As a rule, the amount of information conveyed is directly proportional to the degree of specificity the parasite exhibits for the host preceding the elasmobranch.

Because of the requirement of a polyxenous life cycle, only the following parasite groups have the potential to be informative with respect to host feeding biology: Aspidocotylea, Digenea, and Eucestoda (tapeworms), and those members of the phylum Nematoda that possess one or more hosts in addition to the elasmobranch in their life cycles. Their high prevalence in elasmobranchs, along with the distinct morphology of their plerocercoids, makes tapeworms one of the best parasite groups for indicating feeding biology. Unfortunately their usefulness is extremely limited by our current lack of knowledge regarding complete tapeworm life cycles.

Examples: As part of a faunistic survey of France and its surrounding waters Joyeux and Baer (1936) investigated the cestodes. Their study is particularly useful because the survey involved examination of a wide range of hosts, including both invertebrates and vertebrates, and therefore resulted in some of the most complete information on cestode life cycles available for any single geographic area. All of the examples about the diet of elasmobranchs discussed below are drawn from this survey.

The trypanorhynch tapeworm *Sphyriocephalus tergestinus* Pintner 1913 was found as an adult in *Alopias vulpinus* (Bonnaterre 1788) (Table 1). Despite the hundreds of organisms examined, the last larval form, or plerocercoid, of *S. tergestinus* was found only in the teleost *Lepidopus argenteus* Bonnaterre 1788. Thus, it can be concluded that individuals of *A. vulpinus* parasitized by adults of *S. tergestinus* have been eating the final intermediate host for this tapeworm, *L. argenteus*.

As a second, comparatively less informative example, the dibothridean tapeworm *Echinobothrium typus* van Beneden 1849 was found as an adult in a number of skate species (Table 1). The plerocercoids of this tapeworm were found only in the following three crustacean taxa: *Gammarus locusta*, *Oediceros longimanus*, and a species of *Crangon* Weber 1795. Thus, it can be concluded that skates parasitized by *E. typus* have been eating one or more of these crustaceans. Note that the specificity of the adult tapeworm is not important.

In both of the above instances the fairly tight host specificity of the plerocercoids results in the presence of the adult tapeworm being a reasonably exact indicator of at least some of the food consumed by the elasmobranch. However, in parasite systems lacking host specificity this is not the case. The following is an example of a parasite that, owing to the nonspecificity of the plerocercoid, is relatively uninformative. Adults of the trypanorhynch tapeworm *Nybelinia lingualis* (Cuvier 1817) were found in a number of elasmobranch species. The plerocercoids of this tapeworm were found in five cephalopod and no fewer than 18 teleost species (Table 1). Thus, discovery of *N. lingualis* in the elasmobranch indicates only that the individual has been eating one or more of the five cephalopods and/or one or more of the 18 teleost species.

In addition to providing information on the general feeding biology of elasmobranchs, parasites may also be useful as indicators of size-related changes in elasmobranch feeding habits. In this case it is useful if a number of different polyxenous parasites can be considered simultaneously, and it is particularly helpful if details of the life cycles (especially the final pre-elasmobranch host) are known for as many of these parasite species as possible.

Table 1.
Host records for selected elasmobranch tapeworms from coastal France (from Joyeux and Baer 1936).

Parasite	Definitive host	Final intermediate-host
Sphyriocephalus tergestinus	*Alopias vulpinus*	*Lepidopus argenteus*
Echinobothrium typus	*Raja fullonica*	*Gammarus locusta*
	R. clavata	*Oediceros longimanus*
	R. asterias	*Crangon* sp.
	R. punctata	
	Trygon pastinaca	
Nybelinia lingualis	*Mustelus asterias*	*Sepia fillouxi*
	Galeorhinus galeus	*S. officinalis*
	Scyliorhinus stellaris	*Ommatostrephes* sp.
	Isurus oxyrinchus	*Loligo loligo*
	Squalus acanthias	*Octopus vulgaris*
	Raja oxyrhyncha	*Conger vulgaris*
	R. batis	*Soleo vulgaris*
	R. rubis	*Rhombus maximum*
	R. fullonica	*Mullus barbatus*
	R. clavata	*Scomber scombrus*
	R. punctata	*Pelamys sarda*
		Echneis remora
		Zeus faber
		Caranx trachurus
		Naucrates ductor
		Uranoscopus scaber
		Merlangus virens
		Lota molra
		Trigea lucerna
		T. gurnardus
		Serranus cabrilla
		Xiphias gladius
		Lepidopus lingualis

The following example was provided by Dr. T. Mattis (1843 Ebenezer Rd., Knoxville, TN 37922, pers. commun., Dec. 1987) (Table 2). Two species of tapeworms have been found in individuals of *Dasyatis americana* Hildebrand and Schroeder 1928 with disk diameters of less than nine inches. These include *Acanthobothrium lineatum* Campbell 1969 and *Rhinebothrium lintoni* Campbell 1970. The final intermediate-hosts for the former species are thought to include a number of amphipod species. The final intermediate-host for the latter species is unknown. Individuals of *D. americana* with disk diameters of nine to 18 inches are parasitized by the following tapeworm species: *Rhinebothrium corymbum* Campbell 1975; *Rhodobothrium pulvinatum* Linton 1889; *Acanthobothrium brevissime* Linton 1908; *Onchobothrium uncinatum* (Rud. 1819); and *Prochristianella hispida* (Linton 1890). Unfortunately, the final intermediate-hosts are not known for any but the last species which has been found in penaeid shrimps (Overstreet 1978). Finally, individuals with disk diameters of 19–52 inches have been found infected with the following species of tapeworms: *Phyllobothrium centrurum*

Table 2.
Tapeworms as indicators of size-related changes in the feeding biology of *Dasyatis americana* (from T. Mattis, personal communication).

Size (disk diameter in inches)	Parasites	Final intermediate-host
<9	*Rhinebothrium lintoni*	Amphipod
	Acanthobothrium lineatum	?
9–18	*Rhinebothrium corymbum*	?
	Rhodobothrium pulvinatum	Mollusc
	Acanthobothrium brevissime	?
	Onchobothrium uncinatum	?
	Prochristianella hispida	Penaeid shrimp
19–52	*Phyllobothrium centrurum*	?
	Rhinebothrium maccallumi	Pelecypod
	Acanthobothrium americanum	?
	A. paulum	?
	Parachristianella monomegacantha	Teleost

(Southwell 1925); *Rhinebothrium maccallumi* (Linton 1924); *Acanthobothrium americanum* Campbell 1969; *A. paulum* Linton 1890); and *Parachristianella monomegacantha* Kruse 1859. *Rhinebothrium maccallumi* is known to use pelecypods as the final intermediate-host. The final larval forms of *Parachristianella* monomegacantha have been found in teleosts. The final intermediate-hosts of the other species are not known. Thus, although the life-cycle data are sketchy, a general trend in the diet of *Dasyatis americana* from amphipods to penaeid shrimps and finally to molluscs and teleosts can be inferred from these parasite data.

As a second example, Thoney and Burreson (1986) found that only those individuals of the bullnose ray *Myliobatis freminvillei* Lesueur with disc diameters greater than 68 cm were infected with the aspidocotylean *Multicalyx cristata*. From this parasite evidence these authors suggested that the rays do not feed on the mollusc intermediate hosts or teleost paratenic hosts until they reach a minimum size.

3. Predators

Some parasites may be informative about predators of elasmobranches (usually other large elasmobranchs). Such parasites must satisfy the following conditions: 1) They must be polyxenous, requiring at least one other host in addition to the prey elasmobranch species; 2) The prey elasmobranch must be a required host in the parasite life cycle, making it the only possible source of infection for the predator (otherwise, the presence of a larval parasite in a prey elasmobranch may only indicate what the elasmobranch eats, rather than what eats it); 3) The prey elasmobranch must play the role of an intermediate host, i.e., it must not represent the final host in the parasite life cycle or the parasite cannot be informative with respect to predators of the elasmobranch; 4) The final larval form of the parasite in the elasmobranch must be identifiable (preferrably to species); 5) The parasite must be specific for the definitive (final) host for the amount of information conveyed is directly related to the degree of specificity the parasite exhibits for the definitive host.

As with the previous section the requirement of a polyxenous life cycle results in only the following parasite groups being potentially informative with respect to the predators of elasmobranchs: Aspidocotylea, Digenea, Eucestoda, and those members of the phylum Nematoda that possess one or more hosts in addition to the elasmobranch in their life cycles. As the members of a number of these groups occur only as adults in elasmobranchs, they are inappropriate as indicators in this instance and can be eliminated. For example, this appears to be true for both the Digenea and the Aspidocotylea. However, larval nematodes and larval cestodes have been found parasitizing elasmobranchs, establishing both of these groups as potential indicators of the predators of elasmobranchs.

Example: This example is also drawn from the work of Joyeux and Baer (1936). Plerocercoids of the trypanorhynch tapeworm *Dibothriorhynchus megacephala* (= *Hepatoxylon squali* Martinière 1797) were found parasitizing the following elasmobranch species: *Heptranchias perlo* (Bonnaterre 1788); *Hexanchus griseus* (Bonnaterre 1788); *Scyliorhinus canicula* (L. 1758); *S. stellaris* (L. 1758); *Galeus melastomus* Rafinesque 1810; *Mustelus mustelus* (L. 1758); *Galeorhinus galeus* (L. 1758); *Prionace glauca* (L. 1758); and *Torpedo marmorata* Risso 1810. Plerocercoids were also recovered from the teleosts *Merlangus virens* Cloquet 1824 and *Xiphias gladius* L. 1758. Adults of *D. megacephala* were recovered from *Carcharodon carcharias* (L. 1758). According to this information there is a strong possibility that one or more of these intermediate host elasmobranch species is eaten by the definitive host *C. carcharias*, thus completing the tapeworm life cycle. Unfortunately, because we lack sufficient information as to whether or not these prey elasmobranchs are required in the parasite life cycle (condition 2 above), the possibility that one of the teleosts, such as *Xiphias gladias*, is the usual and perhaps even sole appropriate final-intermediate host for the parasite cannot be eliminated. If this is the case, the presence of plerocercoids in the elasmobranch species tells us nothing about their predators. It simply reflects the similarity of their feeding habits to those of the teleosts, indicating that both groups eat the intermediate host species in which the larval form preceding the plerocercoid develops.

4. Identification

Parasites with the potential to assist with the identification of elasmobranchs must satisfy only a single criterion. They

Table 3.
Host specificity in some microbothriid parasites of elasmobranchs.

Microbothriid species	Elasmobranch host species	Reference
Dermopthirius maccallumi	*Carcharhinus leucas*	Watson and Thorson 1976
D. nigrellii	*Negaprion brevirostris*	Cheung and Ruggieri 1983
D. carcharhini	*Carcharhinus altimus*	Benz 1987
	C. obscurus	Benz 1987
	C. galapagoensis	Benz 1987
	C. limbatus	Benz 1987
	C. brevipinna	Benz 1987
D. penneri	*Carcharhinus brevipinna*	Benz 1987
	C. limbatus	Benz 1987
Dermophthirioides pristidis	*Pristis pectinata*	Cheung and Nigrelli 1983
Neodermophtherius harkemai	*Negaprion brevirostris*	Price 1963

must exhibit specificity for the elasmobranch host. In general the amount of information conveyed is directly proportional to the degree of specificity the parasite exhibits for the elasmobranch host.

Because host specificity is the only criterion, members of any of the four major phyla may be useful with respect to the identification of their elasmobranch host species. For purposes of quick identification, large, ectoparasitic groups such as some of the Arthropoda and the Mongenea are most appropriate. Unfortunately, generalizations regarding the usefulness of subgroups within the four major parasite phyla are limited by our extreme lack of knowledge regarding host specificity in the majority of the elasmobranch parasite groups.

Examples: A number of species belonging to the monogenean family Microbothriidae appear to be sufficiently host-specific (Table 3) to aid with the identification of their elasmobranch hosts. For example, according to Price (1963), *Neodermoptherius harkemai* Price 1963 has only been reported from *Negaprion brevirostris* (Poey 1886). If host specificity in this species is actually as tight as current records indicate, discovery and identification of this parasite will allow corroborative identification of the host.

This kind of indirect identification can be helpful in situations where, for example, parasites were collected and elasmobranch identification data were lost or incomplete. In some instances, parasite inferred host identifications can save effort. For example, Benz (University of British Columbia, 6270 Univ. Blvd., Vancouver, B.C. V6T 2A9, pers. commun., Dec. 1987) has used the pattern of ectoparasitic copepods to identify elasmobranchs caught by hook and line, while they were still in the water. In such cases effort need not be wasted landing undesirable elasmobranch species.

5. Phylogeny

The assumption inherent in any methodology that uses parasites as indicators of elasmobranch phylogeny is that at least some coevolution has occurred between the parasites and their elasmobranch hosts. Three methodologies of varying degrees of complexity and perhaps dependability have been outlined in the literature. The first is direct inference from host specificity data. The second is generation of host phylogenies or branching diagrams using cladistic analysis of parasite presence/absence data. The third is generation of host phylogenies using cladistically generated parasite phylogenies in combination with parasite presence/absence data. The only requirement for the parasites is that they exhibit a certain degree of host specificity, thus members of all four major phyla parasitic on elasmobranchs are potential sources of information.

A. Direct Inference from Host-Specificity Data—This is the simpliest, most frequently used, and probably the least dependable of the three techniques. This technique depends essentially on the assumption that the host specificity of the parasite is a direct indicator of the relationships of the hosts. For example, the monogenean *Dermopthirius penneri* Benz 1987 is currently known to parasitize only two species of host: *Carcharhinus brevipinna* (Müller and Henle 1839) and *C. limbatus* (Valenciennes 1839) (Benz 1987). This parasite therefore supports the hypothesis that these two elasmobranch species are closely related, potentially sister-groups (each other's closest relatives).

This technique is more convincing when two or more different parasite groups are used to make inferences about the same elasmobranch host group. For example, the four tapeworm species currently recognized in the genus *Phoreiobothrium* Linton 1889 have only ever been reported from elasmobranch species belonging to the families Carcharhinidae Jordan and Evermann 1896 and Sphyrnidae Gill 1872 (see Caira 1985). In addition, all thirteen species in the copepod genus *Kroyeria* van Beneden 1853 have only been reported from species belonging to the families Carcharhinidae, Sphyrnidae, and occasionally Triakidae Gray 1851 (see Deets 1987). Thus, both parasite groups independently support the hypothesis that the Carcharhinidae and the Sphyrnidae are closely related. The host records of the copepod genus suggest that the Triakidae may also be closely related to these two families.

Caution should be exercised however in making these kinds of inferences because it is apparent that not all parasite groups are host specific and therefore may not be equally informative about host relationships. For example, the leech *Stibarobdella macrothela* (Schmard 1861) has been reported from at least the following host species:

Carcharhinus falciformis (Bibron 1839); *C. leucas*; *C. limbatus*; *C. obscurus* (LeSueur 1818); *C. springeri* (Bigelow and Schroeder 1944); *C. longimanus* (Poey 1861); *Sphyrna tudes* (Valenciennes 1822); *Ginglymostoma cirratum* (Bonnaterre 1788); and *Paralichthys dentatus* (L.) (Sawyer et al. 1975). From these records, using the same logic as above, this parasite supports the hypothesis that these eight elasmobranch species and one teleost species are closely related!

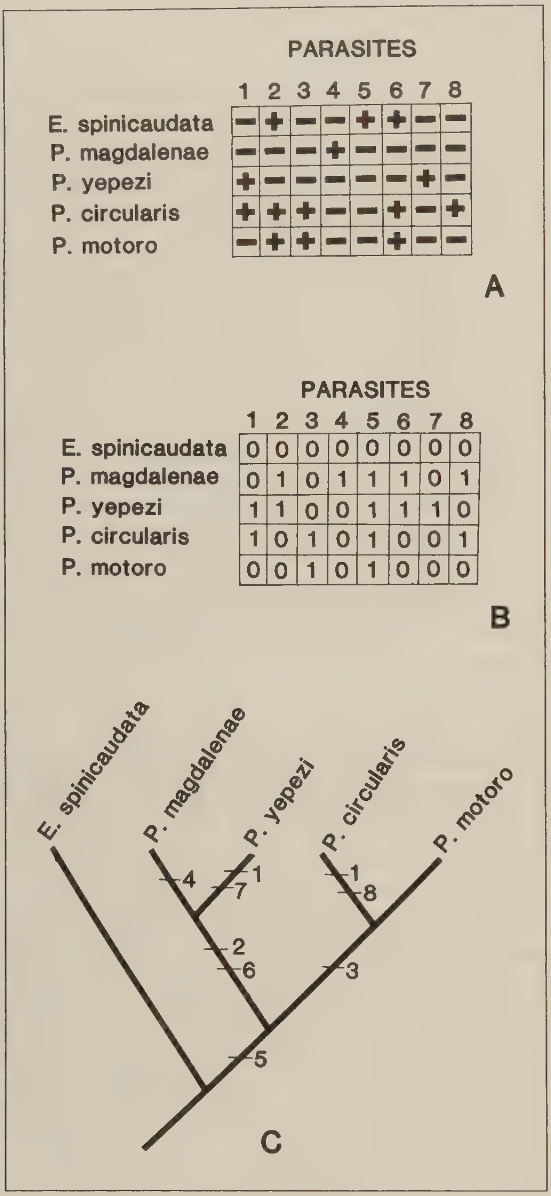
B. Phylogenetic Analysis of Parasite Presence/Absence Data—This method is more involved than simply inferring host relationships from parasite host-specificity data. It is a more rigorous technique that uses data from a number of different parasite species to generate explicit hypotheses of host relationships. It does, however, have a few shortcomings. Under certain circumstances, this technique will not generate the correct tree of host relationships even where there has been strict cospeciation (Brooks 1981).

For the ingroup, or group of elasmobranches whose relationships are to be studied, a matrix is constructed that summarizes which parasite species are found in which of the elasmobranch species under consideration. These parasite presence/absence data are polarized with data on the presence or absence of the same parasites in one or more "outgroup" elasmobranch taxa. Although any elasmobranch species not included in the ingroup would be appropriate, members of groups closely related to the elasmobranch group being analyzed make the best outgroup species. For example, if one is examining relationships within a family of sharks, it would be best to use members of several other families of sharks (preferably families thought to be closely related to the ingroup family) as members of the outgroup, rather than several ray or skate species. Elasmobranch species that potentially belong to the family under consideration are inappropriate as members of the outgroup. In general, parasites present in the outgroup elasmobranch taxa are considered to be plesiomorphic and the presence/absence matrix is polarized or evaluated with this in mind. The matrix of polarized parasite presence/absence data is then subjected to a cladistic analysis. The result is an explicit hypothesis of the phylogenetic relationships of the elasmobranch hosts. Step by step instructions for performing a cladistic analysis were presented by Brooks et al. (1984). In addition, a number of computer packages are available for performing cladistic analyses (e.g., P.A.U.P., by D. Swofford, Illinois Natural History Survey). An excellent discussion of the theory and practice of phylogenetic systematics was presented by Wiley (1981).

Example: In order to demonstrate this method, I will draw on a subset of the data presented by Brooks (1981) with respect to the relationships among four species of freshwater stingrays in the genus *Potamotrygon* Garman 1877 including *P. magdalenae* Dumeril 1865, *P. yepezi* Castex and Castello 1970, *P. circularis* Garman, and *P. motoro* (Müller and Henle 1841). The outgroup to be considered is a species of stingray outside of the genus *Potamotrygon*, *Elipesurus spinicaudata*. The presence/absence matrix for eight species of parasites in the four ingroup and one outgroup elasmobranch host species is shown in Figure 23A. In this matrix a plus sign indicates the presence of a parasite, and a minus sign indicates the absence of a parasite in each elasmobranch species. The results of polarizing the presence/absence matrix using data on the parasites of *E. spinicaudata* are given in the matrix in Figure 23B. Note that regardless of whether a parasite was present or absent in an elasmobranch of the ingroup, the state found in the outgroup is coded with a zero and the alternate state is coded with a one. The phylogenetic tree of hypothesized relationships among the four species of *Potamotrygon* resulting from a cladistic analysis of the matrix in Figure 23B is given in Figure 23C. Numbers correspond to the parasites. Thus, for example, based on these parasite data, *P. magdalenae* and *P. yepezi* are more closely related than either is to the other two species of *Potamotrygon* considered in this analysis.

C. Phylogenetic Analysis of Parasite Presence/Absence Data in Combination with Parasite Phylogenies—This method, entitled "Hennig's Parasitological Method" by its developer Brooks (1981), is even more involved than the previous one. In addition to parasite presence/absence data, data on the phylogenetic relationships among the parasites are incorporated into the analysis. This is the newest technique for using parasite data to generate hypotheses of host relationships, but important improvements continue to be suggested (see O'Grady and Deets 1987). Since its development, this technique has been used to generate parasite-derived cladograms for several elasmobranch groups (for example, Deets 1987; Deets and Ho 1988; Dojiri and Deets 1988).

This technique is similar to the method outlined in section B above, up to the generation of the host-parasite presence/absence matrix. In addition to this matrix, cladograms, or phylogenetic hypotheses, for each of the parasite groups are necessary. These parasite cladograms are translated into data matrices using any one of several methods designed to retain nodal information (O'Grady and Deets 1987). Additive binary coding (Farris et al. 1970) will be demonstrated here. The topology of any cladogram can be completely recovered from an additive binary matrix. The host-parasite presence/absence matrix is then expanded by substituting the additive binary coding from the appropriate additive binary matrix for each parasite species. This expanded host-parasite binary matrix is then polarized as above using the outgroup elasmobranch species, and is cladistically analyzed. The result once again is a hypothesis of the phylogenetic relationships of the elasmobranchs under consideration.



PARASITES

	1	2	3	4	5	6	7	8
E. spinicaudata	−	+	−	−	+	+	−	−
P. magdalenae	−	−	−	+	−	−	−	−
P. yepezi	+	−	−	−	−	−	+	−
P. circularis	+	+	+	−	−	+	−	+
P. motoro	−	+	+	−	−	+	−	−

A

PARASITES

	1	2	3	4	5	6	7	8
E. spinicaudata	0	0	0	0	0	0	0	0
P. magdalenae	0	1	0	1	1	1	0	1
P. yepezi	1	1	0	0	1	1	1	0
P. circularis	1	0	1	0	1	0	0	1
P. motoro	0	0	1	0	1	0	0	0

B

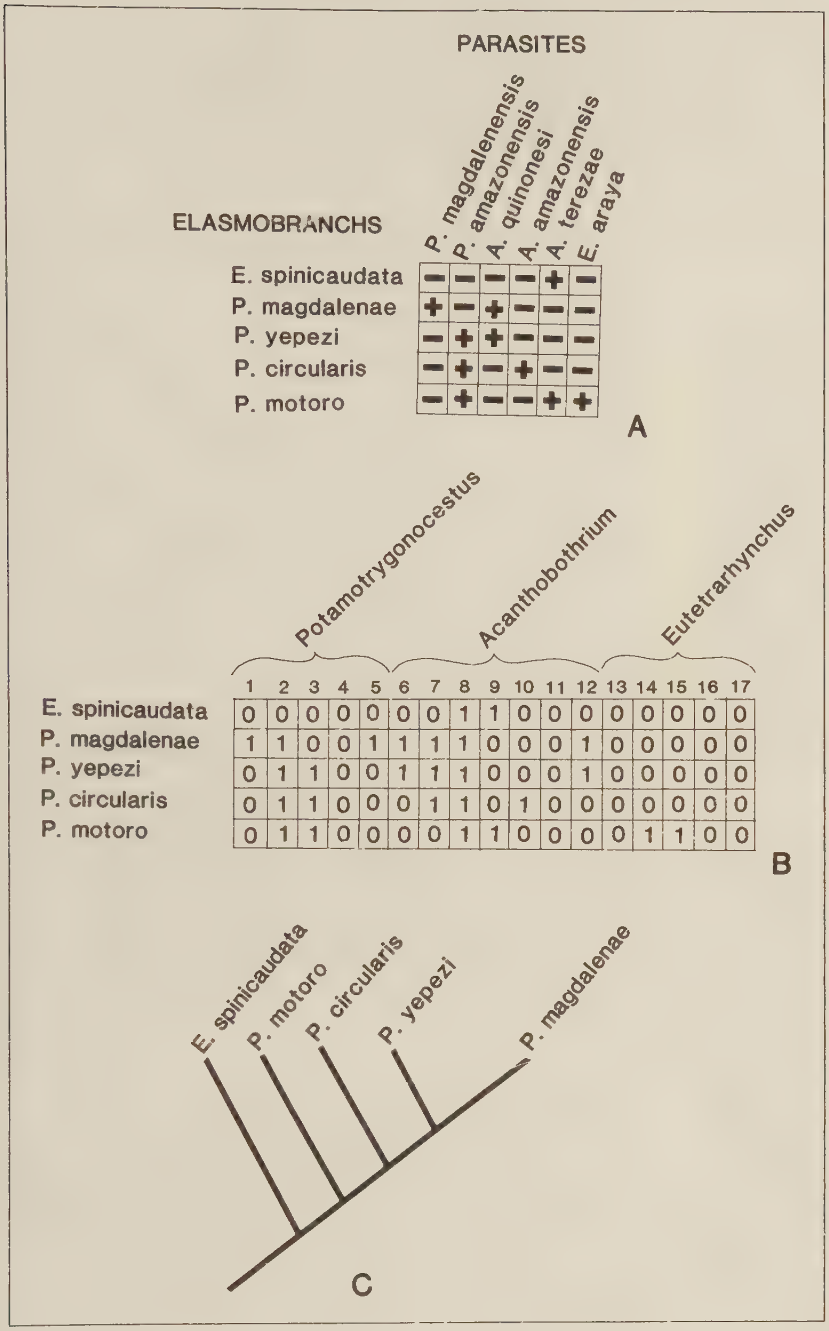
Figure 23.

Steps in cladistic analysis of *Potamotrygon* parasite presence/absence matrix to generate hypothesis of host relationships. A. Host-parasite presence/absence matrix, + indicates presence and – indicates absence of parasite species, modified from Brooks (1981). B. Binary presence/absence matrix polarized using parasites in outgroup host species *Elipesurus spinicaudata*. C. Hypothesis of relationships among four species of *Potamotrygon* resulting from cladistic analysis of matrix in B. Numbers correspond to parasites in A: 1—*Echinocephalus daileyi*, 2—*Rhinebothrium paratrygoni*, 3—*Eutetrarhynchus araya*, 4—*Acanthobothrium quinonesi*, 5—*A. terezai*, 6—*Rhinebothroides scorzai*, 7—*Potamotrygonocestus amazonensis*, 8—*Terranova edcaballeroi*. P = *Potamotrygon*, E = *Elipesurus*.

Example: In order to demonstrate this method, I will draw from a different subset of the data presented by Brooks (1981) with respect to the relationships among four species of stingrays in the genus *Potamotrygon*. Once again the outgroup to be considered will be *Elipesurus spinicaudata*. The parasites on which the analysis will be based in this example include six species of tapeworms in the genera *Potamotrygonocestus* Brooks and Thorson 1976, *Acanthobothrium* van Beneden 1849, and *Eutetrarhynchus* Pintner 1913. I have chosen these particular groups primarily because hypotheses of relationships have already been published for these three genera (Brooks et al. 1981).

The presence/absence matrix for the distribution of these six species of parasites in the four ingroup and one outgroup elasmobranch species is shown in Figure 24A. Partial cladograms and their corresponding additive binary matrices, for each of the three parasite genera, are given in Figures 25–27. The expanded host-parasite presence/absence matrix with substituted additive binary coding is given in Figure 24B. An example of this substitution is as follows. According to the original presence/absence matrix (Fig. 24A) *Potamotrygon circularis* is parasitized by *Potamotrygonocestus amazonensis* Mayes, Brooks and Thorson 1981, and *Acanthobothrium amazonensis* Mayes, Brooks and Thorson 1978, but not by any species of *Eutetrarhynchus*. Therefore the row for this host species (row 4 in Fig. 24B), is coded for *P. amazonensis* with the sequence "01100" corresponding to this species in the additive binary matrix for *Potamotrygonocestus* (Fig. 25B), and is coded for *A. amazonensis* with the sequence "0110100" corresponding to this species in the additive binary matrix for *Acanthobothrium* (Fig. 26B). As *P. circularis* is not parasitized by *Eutetrarhynchus araya* (Woodland 1934) it is coded with the sequence "00000" for *Eutetrarhynchus*. The hypothesis of phylogenetic relationships among the four ingroup stingray species, resulting from a cladistic analysis of the expanded matrix given in Figure 24B after consideration of the outgroup states, is shown in Figure 24C.

At this point I would like to emphasize that each of these techniques for using parasite data to establish hypotheses of relationship among their elasmobranch hosts should be used with caution. None of the techniques is foolproof. All contain subjective components and it is important that as much parasite data as possible be incorporated into the analysis. To emphasize this point, in my examples I deliberately chose subsets of the parasite data of Brooks (1981) that result in different elasmobranch cladograms. In the future, in order for the parasite-implied relationships among these four species of *Potamotrygon* to be thoroughly investigated, all of the available parasite data should be carefully evaluated. In addition, consideration should be given to further collections of parasites from these elasmobranchs in view of the preliminary state of our current knowledge of the parasite assemblage in these species.



PARASITES

ELASMOBRANCHS	P. magdalenensis	P. amazonensis	A. quinonesi	A. amazonensis	A. terezae	E. araya
E. spinicaudata	−	−	−	−	+	−
P. magdalenae	+	−	+	−	−	−
P. yepezi	−	+	+	−	−	−
P. circularis	−	+	−	+	−	−
P. motoro	−	+	−	−	+	+

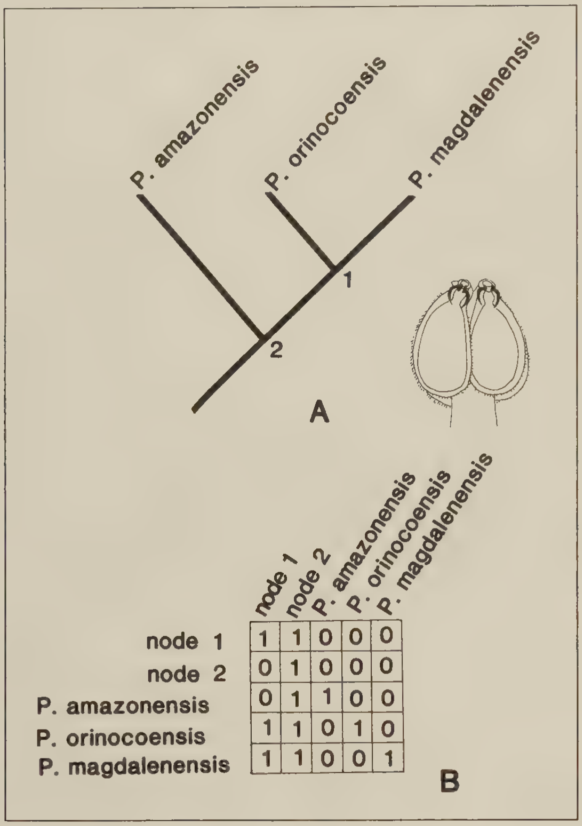
	Potamotrygonocestus					Acanthobothrium							Eutetrarhynchus				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
E. spinicaudata	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
P. magdalenae	1	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0
P. yepezi	0	1	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0
P. circularis	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0
P. motoro	0	1	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0

Figure 24.
Steps in cladistic analysis using parasite relationships in combination with *Potamotrygon* parasite presence/absence matrix. A. Host-parasite presence/absence matrix, + indicates presence and − indicates absence of a parasite species. B. Expanded matrix after substitution of appropriate additive binary coding from Figures 21–23 for presence of each parasite species, modified from Brooks et al. (1981). C. Hypothesis of relationships among four species of *Potamotrygon* resulting from cladistic analysis of matrix in B. Elasmobranchs: E = *Elipesurus*, P = *Potamotrygon*. Parasites: P = *Potamotrygonocestus*, A = *Acanthobothrium*, E = *Eutetrarhynchus*.

6. Origins and Ancient Distributions

Until recently, discussions on the origins and ancient distributions of hosts based on their parasites have been very subjective. The literature contains a number of generalized rules that have been suggested in an attempt to assist with the unravelling of questions about ancient conditions. For example, Manter (1966) dealt with the use of parasites as indicators of ancient times and proposed that: 1) a host will have a greater variety of parasites in the region where it has lived the longest, usually its place of origin; and 2) if a host was once broadly distributed for a long period of time, it might be expected to retain similar populations of parasites following isolation or disruption of its distribution. However, rules such as these depend upon assumptions that may not necessarily be true, such as the suggestion that parasites generally speciate more slowly than their hosts.

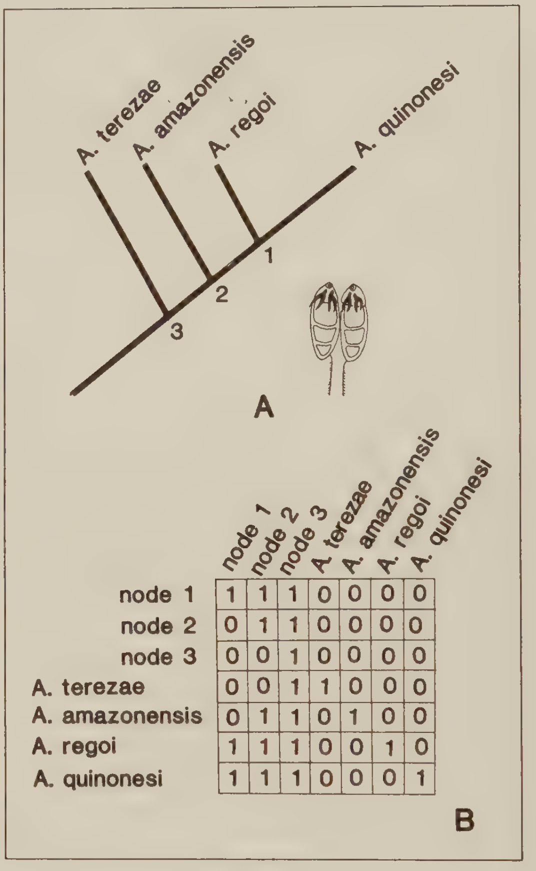
Recently, the trend has been towards developing more rigorous techniques with which to investigate questions of host origins and ancient distributions. Several studies have consisted of the use of cladistic analysis of parasite taxa


P. amazonensis
P. orinocoensis
P. magdalenensis
1
2
A
B

	node 1	node 2	P. amazonensis	P. orinocoensis	P. magdalenensis
node 1	1	1	0	0	0
node 2	0	1	0	0	0
P. amazonensis	0	1	1	0	0
P. orinocoensis	1	1	0	1	0
P. magdalenensis	1	1	0	0	1

Figure 25.

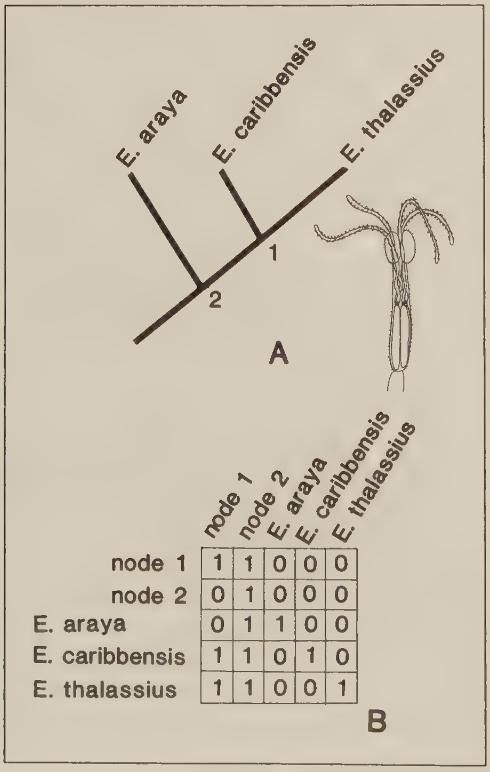
A. Hypothesis of relationships among three species of tapeworms in *Acanthobothrium*, modified from Brooks et al. (1981). B. Matrix of additive binary coding representing cladogram in A.


A. terezae
A. amazonensis
A. regoi
A. quinonesi
1
2
3
A
B

	node 1	node 2	node 3	A. terezae	A. amazonensis	A. regoi	A. quinonesi
node 1	1	1	1	0	0	0	0
node 2	0	1	1	0	0	0	0
node 3	0	0	1	0	0	0	0
A. terezae	0	0	1	1	0	0	0
A. amazonensis	0	1	1	0	1	0	0
A. regoi	1	1	1	0	0	1	0
A. quinonesi	1	1	1	0	0	0	1

Figure 26.

A. Hypothesis of relationships among four species of tapeworms in *Acanthobothrium*, modified from Brooks et al. (1981). B. Matrix of additive binary coding representing cladogram in A.


E. araya
E. caribbensis
E. thalassius
1
2
A
B

	node 1	node 2	E. araya	E. caribbensis	E. thalassius
node 1	1	1	0	0	0
node 2	0	1	0	0	0
E. araya	0	1	1	0	0
E. caribbensis	1	1	0	1	0
E. thalassius	1	1	0	0	1

Figure 27.

A. Hypothesis of relationships among three species of tapeworms in *Eutetrarhynchus*, modified from Brooks et al. (1981). B. Matrix of additive binary coding representing cladogram in A.

in view of specific hypotheses about the corresponding host taxa. The only requirement of this kind of procedure is that the parasites exhibit a certain degree of host specificity, thus, all four of the major phyla of elasmobranch parasites are potentially informative about elasmobranch origins and ancient distributions.

With respect to elasmobranchs, I am aware of only a single study where this procedure has been attempted. Brooks et al. (1981) ambitiously endeavored to answer five questions dealing with the origins and ancient distributions of the freshwater stingrays in the genus *Potamotrygon*. Their questions included 1) Is the genus monophyletic or polyphyletic? 2) Does it have its origin in fresh or marine waters? 3) If it is marine in origin, is it from the Atlantic or the Pacific? 4) What is the sister-group of the genus; and 5) Can the distribution be explained with dispersal or vicariance? In other words, did these stingrays (or their ancestors) actively move into the areas that they currently inhabit, or is the current distribution of these species the result of a physical splitting of a previous distribution with vicariant events such as Andean orogeny. In order to answer these questions about the stingrays, Brooks et al. (1981) performed a cladistic analysis on each of the parasite groups found in these rays along with some of the closest relatives of these parasites. They also tabulated the hosts and geographic distributions of the parasites and their closest relatives. All of these data were considered in light of assertions extending from hypotheses consisting of combinations of their five questions. They concluded that the potamotrygonids represent a monophyletic group whose ancestor was a nondasyatid marine stingray from the Pacific which was trapped in South America by Andean orogeny.

Unfortunately, careful examination of the data presented by Brooks et al. (1981) causes one to question their conclusions. The parasite distributions were far from unambiguous, and it is unclear as to exactly how they knew they were making decisions based on the closest relatives of parasites of the potamotrygonids when, in most cases, only some of the species in each of the parasite genera were included in each cladistic analysis. In addition, by combining expectations about the five questions into four complex hypotheses, numerous assumptions were introduced, none of which was thoroughly dealt with. I suggest that this particular system should be reevaluated before the conclusions of Brooks et al. (1981) are generally accepted.

Conclusions

Elasmobranch parasites can be useful in inferring information about the following features of the biology of their hosts: Geographic movements and migrations, feeding biology, predators, identification, phylogenetic relationships, and origins and ancient distributions. Not all parasite species are appropriate as indicators of all six of these aspects. In choosing appropriate parasite indicators, the biology of each parasite group should be taken into consideration. Because of the current dearth of information on the parasites of elasmobranchs in general, the potential of these organisms as biological indicators is certainly far from being realized. The situation can only improve as research on elasmobranch parasites and their implications for elasmobranch biology continues.

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Shark Reproductive Strategies as a Limiting Factor in Directed Fisheries, with a Review of Holden's Method of Estimating Growth-Parameters

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ABSTRACT

An historical examination of shark fisheries characterizes them as "boom and bust" enterprises. The reproductive strategies of elasmobranchs—e.g., a small number (2–135) of large young (100–1000 mm) are born after a gestation period of 0.5 to 2.0 years, and first maturity follows at a late age—require a long time for stocks to recover from the effects of directed fisheries. The rational exploitation of shark populations can be accomplished only through careful management. A review of the reproductive and growth parameters of shark species is undertaken which can be used to indicate species vulnerability to directed fisheries. A comparison of historical predictions of K values with recent empirically derived K values indicate that past methods cannot be applied universally and may not work at all. Future research to assess the potential of elasmobranch fisheries should address early life-history requirements, minimum reproductive biomass, and should examine the adaptations (if any) of elasmobranch fecundity and natural mortality to fluctuations in stock abundance and food supply.

Introduction

Sharks have always been of interest to man, and shark fishing has had a long and varied history. The fisheries have typically been small and even more inconstant in nature than teleost fisheries. Regard for sharks as food has varied from culture to culture, but as the flesh is wholesome, boneless, and mild in taste, directed fisheries for food occur from time to time. Sharks have also been harvested for their fins, skin, teeth, liver oil, cartilage and medicinal products. Historically, directed fisheries for sharks have been characterized as "boom and bust" enterprises, because populations have been rapidly reduced to levels that will not support the fishery. Populations impacted by shark fisheries are slow to recover, sometimes requiring decades to reach their former levels. Holden (1974, 1977) provides excellent overviews of the problems with elasmobranch fisheries and offers as examples the earlier fisheries for the spiny dogfish, *Squalus acanthias*; the California soupfin, *Galeorhinus galeus*; and skates and rays in British waters. More recently, Bedford (1987) describes problems of contemporary U.S. fisheries for the common thresher shark, *Alopias vulpinus*, and the shortfin mako shark, *Isurus oxyrinchus*.

The world interest in using sharks continues and mankind's increasing demand for marine resources and growing efficiency at harvesting the sea underscores the need for development of new shark fisheries and better management of existing fisheries based on scientific knowledge of sharks, their life histories, and the effects fisheries are likely to have on the populations. We propose to review the reproductive limitations of shark populations as they relate to fisheries, to examine critically Holden's (1974) work and to investigate factors which contribute to overexploitation in shark fisheries.

Reproductive Strategies of Selachians

The principle reason that shark fisheries are short-lived, or of low production, is that elasmobranchs exhibit several conservative reproductive strategies often seen in combination. Consequently, most stocks do not respond well to fishing techniques that are dependent on burgeoning year classes. Because of these elasmobranch strategies, there is a close relationship between the number of adults (stock) and the number of young produced (recruitment) in most elasmobranchs (Holden 1974). Stock and recruitment of teleost year classes are less directly linked owing to the high fecundity of most adult female bony fishes.

Most sharks produce large young (up to 30% of the parent's maximum length) which have a superior chance to survive individually relative to the progeny of teleosts. The less plesiomorphic sharks retain their young for many months and nourish them in their uteri. Many sharks in temperate to subtropical seas have a gestation period of 11 to 12 months. The known range is 70 to 80 days in *Chiloscyllium griseum* (Dral 1981) to 22 months in *Squalus acanthias* (Holden 1974). Parker and Stott (1965) hypothesized 43 months of gestation for *Cetorhinus maximus* based on the observation of prebirth vertebral rings from free living sharks. No direct evidence is available yet for *Cetorhinus*. Actual gestation for all species is influenced by environmental and physiological conditions. Gestation in warmer seas is, perhaps, a month shorter than in more temperate seas for a particular species.

The litter size of most sharks commonly encountered in fisheries averages between 2 and 16 embryos or ''pups'' with an upper range of over 100. The more fecund species are *Prionace glauca* (82–135 pups) (Gubanov and Grevor'yev 1975; Pratt 1979); *Hexanchus griseus* (108 pups) (Ebert 1986a); *Galeocerdo cuvier* (55 pups) (Castro 1983); and *Galeorhinus galeus* (52 pups) (Castro 1983). There are trends in some species of sharks for larger females to bear more young (*Prionace glauca*) or the same number of larger young (*Alopias*) (Gilmore 1983; Stevens 1983) or perhaps both more and larger young. There seems to be no obvious senescence in the reproductive ability of female sharks. The largest, therefore, are apparently the most fecund. These concepts, however, need corroboration, species by species.

Size at birth ranges to well over 1 meter. *Alopias vulpinus* has embryos recorded at 151 cm total length, but its long tail accounts for nearly half this length. The birth size of *Cetorhinus maximus* was reported to be 167 cm (Aasen 1966a), but the account is inexact. The birth size of *Carcharodon carcharias* is also questionable. Uchida (1987) reported embryos with an estimated length of 100–110 cm. The smallest free-swimming white shark recorded by Casey et al. (1985) was 122 cm. This shark possessed several characteristics of a young of the year shark including basal tooth cusps, translucent trailing edges on the fins and a short groove on the midline between the pectorals. This groove is probably a mark left by the yolk sac which is absorbed prior to the oophagous period.

Typically species of large sharks mature at approximately 2 m and bear 4 to 16 young, which are 30 to 50 cm long at birth. Information on those that have been aged suggests they mature relatively late in life. Apparently, natural mortality rates are low enough in sharks (versus telostean fishes) to allow adequate population maintenance with late maturation.

Several different modes or patterns of embryonic development have arisen in elasmobranchs. Older literature has referred to these as oviparity, ovoviparity, and viviparity. Budker (1958) pointed out that the difference between ovoviparity and viviparity was a matter of degree and was somewhat artificial. He and other researchers, following his observation, have consequently dropped the term ''ovoviparity''. More useful categories have been proposed by Wourms (1977) and Otake (1990). Otake's analysis uses morphological differences of uterine compartment formation, whereas Wourm's uses functional descriptors. Other specialized reproductive structures and life cycles of elasmobranchs are discussed by Wourms (1977, 1981); Taniuchi (1978); Pratt (1979, 1988), and Gilmore (1983, 1985).

Growth Rates and the Calculation of '*K*'

The calculations of growth rates and population age structure are central elements in understanding a fish population's ability to withstand exploitation by a fishery. Growth data are very difficult to obtain for most elasmobranchs. Most contemporary studies of fish age and growth use or at least include the von Bertalanffy Growth Function (VBGF) as a descriptor of growth. The VBGF's decaying exponential curve seems to model the growth of many fish species closely and some of its parameters are applicable to other models. The coefficient *K* from this equation is a unitless quantity similar to slope and rate of growth:

$$1_t = L_\infty \{1 - \exp - K(t - t_0)\}, \qquad (1)$$

where 1_t = length at time t;
L_∞ = the asymptotic length;
K = a constant; and
t_0 = age at zero length.

The empirical length-at-age data needed to calculate *K* with accuracy are available for only a limited number of elasmobranchs. In an attempt to overcome this problem, Holden (1974) modified the VBGF to solve for *K* using a hypothetical t_0. This was a perspicacious and logical step because some of the VBGF parameters may be independently estimated. This method takes advantage of elasmobranch reproductive strategies using gestation time t_0 and length at birth (1_{t+T}). The assumption is made that embryonic growth is a model for postpartum growth. Reproductive strategies are involved because the gestation time, t_0, and the length at birth (1_{t+T}) both enter into the calculations. His first equation became:

$$1_{t+T} - 1_t = (L_\infty - 1_t)\; 1 - \exp(-KT), \qquad (2)$$

where 1_{t+T} = length at time $(t + T)$.

He further modified this to take advantage of assumed elasmobranch gestation times:

$$1_{t+T}/L_{\infty} = 1 - \exp(-KT), \qquad (3)$$

where 1_t = length at conception—0 at zero time;
T = length of gestation or hatching period;
1_{t+T} = length at birth; and
L_{∞} = maximum observed length, or $L_{\max}$.

Holden (1974) used data from Bigelow and Schroeder (1948); Olsen (1954); Parker and Stott (1965); Daiber (1960); Richards et al. (1963); and his own work (Holden 1972, Holden and Meadows 1962) as the basis for his Table 4. Holden concluded that K values were confined to the range 0.1 to 0.2 for selachians and 0.2 to 0.3 for batoids (Holden 1974, table 3). As most gestation periods were not yet known, Holden manipulated KT so that K values for several shark species fell between 0.1 and 0.2, changing gestation times accordingly.

Table 1.
Calculated K values with variable $L_{\max}$ and birth size in total length (cm).

	Carcharodon carcharias		
	Size at birth (cm)		
$L_{\max}$	100	110	122
594	0.184	0.205	0.230
640	0.167	0.187	0.211
823	0.130	0.143	0.160
1113	0.094	0.104	0.116

	Isurus oxyrinchus	
	Size at birth (cm)	
$L_{\max}$	80	81
364	0.248	0.252
610	0.141	0.143

Problems with the Method

If Holden's method is valid, it would be of great value as a quick way to provide (VBGF) parameters where little data has been gathered, as at the beginning of most shark fisheries. However, the accuracy of parameters produced by this method should be examined. Francis (1981) applied the Holden method to *Mustelus canis* and concluded that "Holden's assumption that all sharks have growth constraints [K values] in the range 0.10–0.20 is invalid, and his method for estimating K should only be used when the gestation period has been independently determined."

There are two possible sources of error in Holden's estimates, intrinsic and extrinsic. Intrinsic problems are associated with the peculiarities and bias of the VBGF and its derivative equations. Equation (3) is very sensitive to changes in $L_{\max}$ and size at birth. Table 1 illustrates ranges of K produced by different literature values for $L_{\max}$ at a gestation time of one year. It is becoming apparent to investigators that the VBGF does not fit all shark data well.

Values of t_0 for a slow-growing species such as *Carcharhinus plumbeus* range from −4.5 to −4.9 years (Casey et al. 1985). These are absurd predictions if validity is given to the assumption that intrauterine growth is the same as postpartum growth. In the analysis of Casey et al. (1985) the VBGF is reduced to almost a straight line in *C. plumbeus*. In contrast, the faster growing *Isurus oxyrinchus* (Pratt and Casey 1983) displays the more typical decaying exponential curve with more reasonable VBGF, t_0 values of −1 for both sexes. The applicability of asymtotic growth models and the universality of the VBGF relative to the growth of fishes has been seriously questioned (Knight 1968; Roff 1980). A linear function is probably a better predictive model for some slow growing sharks.

The assumption that intrauterine growth is similar to free living growth is, in most cases, an unsupported one. Embryos of the family Lamnidae are very robust with large yolk stomachs and well nourished bodies. Most other species, even carcharhinids nourished by a placenta, tend to bear full-term embryos that are slender and even "tadpole shaped" with underdeveloped bodies. Long, slender embryos facilitate uterine "packing" and give the newborn those advantages conferred by length—higher speed and a competitive size—but growth of these embryos is often of a different order from that of adult growth. Growth curves of intrauterine embryos are rare. Parsons (1983) shows a curve (figure 14) for *Rhizoprionodon terraenovae* embryos that exhibits differential, almost asymptotic growth "in utero." *R. terraenovae* pups grow first in length, then in bulk, similar to free-living sharks. Projecting Parson's intrauterine growth data past birth gives unrealistic results. Springer (1960) provides estimates of embryonic growth in *C. plumbeus*. Based on these and his own observations, Casey et al. (1985) suggested that the embryonic growth of *C. plumbeus* exhibited a different growth stanza (Ricker 1979) from adult growth.

The extrinsic problems with the Holden estimates are due to limitations in the quantity, veracity, and accuracy of the life history parameters recorded in the literature. Gestation period is a typical example because it is difficult to determine in free-living species. A number of gravid females are needed from different times of the year to provide embryo measurements and enough data to establish the limits of the cycle and its annual periodicity. Gestation time is probably always a range, dependent on water temperature and other environmental parameters.

Size at birth is often reported inaccurately. In species of large sharks and rays, the capture of a gravid female is often a rare event. Because embryos acquire most species characteristics by the middle of the gestation period, many are erroneously reported as full-term. Premature embryos aborted on deck during capture have been mistakenly judged to be full-term owing to the female's ability to release them, their fully formed appearance, and the lack of other embryos for comparison. These circumstances result in low values for size-at-birth estimates, especially where a small range of pregnant females have been examined. Maximum embryo size should be verified with the minimum free-living size.

In a similar circumstance, the number of young born in each pregnancy can easily be mistaken. Many females abort at least some of their young during capture. The number of embryos is consequently underreported. A thorough examination of the uteri can sometimes reveal whether the full complement of embryos is present. Approximately equal numbers of embryos usually occur in each turgid uterus. A partially collapsed uterus with broken uterine compartments and disorganized contents can indicate that birth, or premature parturition, has occurred. In placental species, the number of placentae, or placental remnants, can be counted on the dorsal wall of an inverted uterus to verify the number of embryos in that particular litter.

Accurate data on adult maximum size is difficult to obtain for even common deepwater sharks and pelagic sharks and rays. The problem is compounded by measurement error in both weight and length for very large fish. As would be expected, some maximum reported sizes are gradually increasing as more specimens are observed. A few, notably *Carcharodon carcharias*, are decreasing in size as authors such as Randall (1973, 1987) work at refining the published records. This is because the size of large sharks tends to be exaggerated by observers. The reported total length of *C. carcharias*, for example, has been reduced by Randall from 11.1 m to 5.9 m.

Size at maturity is difficult to determine. If a female is gravid, her maturity is obvious, but most species are not gravid when observed, and the minimum size at maturity can be difficult to establish unless many pregnant females are examined. Flaccid uteri and large ovarian eggs are a clue but do not, of themselves, constitute sexual maturity. Empirically derived age-at-maturity data are available for only a small percentage of species.

Ultimately, the above parameters can be confused by misidentification. Some families of sharks (e.g., Carcharhinidae) comprise similar species that can be difficult for even taxonomists to separate. Observations by an inexperienced worker can obfuscate the literature.

Updating the Life History Parameters

The Holden method has been used frequently by contemporary workers studying age and growth in sharks. With a little data, a few assumptions, and a calculator, a growth curve can be constructed. The biggest assumption is the veracity of the method. In the past, lack of precision in recording life-history parameters has made accurate predictions of growth parameters by any method uncertain. In the fifteen years since Holden's work was published, the gestation period, maximum length, length at birth and number of young of many species of sharks has been observed or determined with accuracy. We have constructed a new summary table (Table 2) with updated species information. This includes Holden's original *K* values, an updated *K* value using Equation (3), empirically derived *K* values from our work and the literature, and other statistics of importance to fisheries workers. We then updated Holden's *K* value using these more recent values. For simplicity and convenience of calculation, we have reported modal values where ranges occur in the literature. Holden varied his gestation period estimate to produce a *K* between 0.1 and 0.2. We have used only known gestation times. Species have been grouped by gestation period, when known, and by family. We have confined this list to species that represent current or historical commercial fisheries interest or, like the white shark, are of special interest to man.

Comparison of Holden's Data and Contemporary Calulations for Sharks

Holden's method assumes a relationship between size at birth, maximum size, gestation period, and *K* that permits the prediction of *K* (Equation (3)). We have used contemporary values from Table 2 to compare these data in Figure 1. The value of *K* is permitted to range outside of Holden's limits of 0.1 to 0.2. Equation (3) (Holden's Method) is used to generate Figure 1a. As would be expected, the plot is a straight line—minor deviations are the result of decimal point rounding. However, when literature derived (independent) *K* values are plotted in Figure 1b, a pattern of points appears that demonstrates little or no trend. If *K* is a function of this ratio, then the empirical plot should have a similar trend line to the one shown in Figure 1a. That it does not, may be due to the lack of precision with which the *K* values have been determined. The parameter *K* is easily derived from a Walford (1946) plot and several computer programs (Fabens 1965; Allen 1966). Results of these programs vary when the same data sets are run, and there is no standard technique for using them. Data sets are often so limited in range or sample size that an accurate *K* may not have been obtained for some species. This qualification not withstanding , Figure 1b could also indicate that the method does not work for all sharks.

We further examined this predictive relationship, by comparing updated parameters derived from Equation (3)

Table 2.

Shark life-history parameters.

Species	Gestation time (months)	Maximum length TL (cm)	Maximum size at birth TL (cm)	Birth size ratio	Female length at maturity TL (cm)	Female age at maturity (years)	Maximum number of young in litter	Calculated *K*		Updated reference source	Empirical *K*	Age and growth reference
								Holden (1974)	Holden updated (1987)			
T = 0.5 Year												
Galeorhinus australis	6	174	30	17	135	10	28	0.095	0.095	Grant et al. (1979) Olsen (1954)	0.164	Grant et al. (1979)
T = 1 Year												
Lamniformes												
Alopias superciliosus	—	450	105	23	350	—	2	0.163	0.266	Gilmore (1983)		
A. vulpinus	9	491	151	31	415	7	4	0.147	0.367	Bedford, pers. comm. 1	0.108	Cailliet et al. (1983)
Carcharodon carcharias	—	594	110	18	457	12	7	0.113	0.205	Authors data Randall (1987)	0.058	Cailliet et al. (1985)
Cetorhinus maximus	18	980	150	15	500	5	6	0.143	0.166	Parker and Stott (1965)	0.110	Parker and Stott (1965)
Isurus oxyrinchus	12	364	80	22	258	7	16	0.143	0.248	Aasen (1966b) Stevens (1983)	0.234	Cailliet, pers. comm. 4 Pratt and Casey (1983)
Lamna nasus	8	365	72	20	225	7.5	4	0.112	0.220	Castro (1983) Aasen (1963)	0.116	Aasen (1963)
Eugomphodus taurus	10.5	318	100	31	237	—	2	0.193	0.378	Thornson and Lacy (1982) Gilmore et al. (1983)		
Carcharhiniformes												
Carcharhinus acronotus	12	176	50	40	113	8	6	0.392	0.440	Schwartz (1984)	0.140	Schwartz (1984)
C. amblyrhynchos	12	255	60	23	137	7.5	6	—	0.268	Compagno (1984)	0.294	De Crosta (1984)
C. brevipinna = maculipinnis	12	196	75	27	180	7	12	0.314	0.314	Branstetter (1987c)	0.212	Branstetter (1987c)
C. falciformis	12	305	70	23	225	9	13	—	0.260	Springer (1960)	0.153	Branstetter (1987a)
C. isodon	12	189	48	25	139	5	6	0.293	0.293	Branstetter (1987a) Branstetter and Shipp (1980)	0.048 0.220	Hoenig (1979) Branstetter, pers. comm. 5
C. leucas	11	300	75	25	225	18	13	0.125	0.288	Branstetter, pers. comm. 2 Thorson and Lacy (1982)	0.039	Hoenig (1979)
C. limbatus	11	180	60	24	155	7	10	0.139	0.278	Branstetter and Stiles (1987) Clark and von Schmidt (1965)	0.076 0.200	Branstetter and Stiles 1987 Killam (1987)
C. longimanus	12	270	75	28	175	—	15	0.186	0.325	Branstetter (1987c) Bass et al. (1973)	0.274 0.040	Branstetter (1987c) Saika and Yoshimuna (1985)
C. obscurus	12	365	100	27	280	—	14	0.171	0.320	Castro (1983) Springer (1960)	 0.034	Branstetter pers. comm. 1 Hoenig (1979)
C. plumbeus = milberti	12	239	56	23	183	13	13	0.133	0.267	Clark and von Schmidt (1965) Springer (1960)	0.014 0.057	Lawler (1976) Casey et al. (1985)
Galeocerdo cuvieri	12	550	85	15	320	10	55	0.106	0.168	Branstetter et al. (1987)	0.057 0.184	Lawler (1976) Branstetter et al. (1987)
Galeorhinus japonicus	10	116	25	19	93	5	22	—	0.242	Tanaka et al. (1978)	0.107	De Crosta (1984)
G. zyopterus	12	200	35	17	170	—	52	0.1	040.192	Castro (1983)	0.200	Tanaka et al. (1978)

Table 2. (continued)

Species	Gestation time (months)	Maximum length TL (cm)	Maximum size at birth TL (cm)	Birth size ratio	Female length at maturity TL (cm)	Female age at maturity (years)	Maximum number of young in litter	Calculated *K*		Updated reference source	Empirical *K*	Age and growth reference
								Holden (1974)	Holden updated (1987)			
T = 1 Year (continued)												
Carcharhiniformes (continued)												
Mustelus californicus	12	163	30	18	70	3	16	—	0.203	Compagno (1984) Yudin (1987)	0.218	Yudin (1987)
M. canis	10	152	39	26	97	2	20	0.149	0.296	Francis (1981)	0.360	Francis (1981)
M. henlei	12	100	28	28	57	3	10	—	0.328	Compagno (1984) Yudin (1987)	0.225	Yudin (1987)
M. manazo	10	96	30	30	13	25	14	—	0.375	Teshima et al. (1971) Tanaka and Mizue (1977)	0.420 0.379	Francis (1981) Tanaka and Mizue (1979)
Negaprion brevirostris	12	320	60	18	243	13	19	0.132	0.208	Brown and Gruber (1988)	0.540	Hoenig (1979)
Prionace glauca	12	383	50	13	218	5	135	0.110	0.140	Pratt (1979)	0.110 0.160	Stevens (1975) Skomal (1987)
Rhizoprionodon terraenovae	11	107	32	30	85	4	7	0.281	0.355	Parsons (1981, 1983)	0.359	Branstetter (1987b)
Sphyrna lewini = diplana	12	309	45	15	250	15	30	0.150	0.160	Branstetter (1987b)	0.054 0.073	Hoenig (1979) Branstetter (1987a)
S. mokarran = Holden's *tudes*	12	560	70	11	300	—	40	0.133	0.133	Castro (1983)		
Other orders												
Squatina californica	10	152	26	17	95	—	11	—	0.188	Natanson (1986)		
Triakis semifasciata	12	198	20	—	100	10	18	0.150	0.106	Smith (1984)	0.072	Cailliet, pers. comm. 6
T = 2 Years												
Squalus acanthias	22	128	26	20	93	25	14	—	0.023	Jones and Green (1977) Beamish and McFarlane (1985)	0.037	Jones and Green (1977)
T = Unknown												
C. galapagensis	—	370	80	22	235	—	16	—	0.244	Compagno (1984)	0.172	De Crosta (1984)
C. oxyrhynchus	—	152	39	26	—	—	4	0.296	0.296	Holden (1974)		
Centroscymnus coelolepis	—	120	30	25	—	—	16	0.230	0.288	Castro (1983)		
Etmopterus hillianus	—	32	9	28	—	—	5	0.330	0.330	Holden (1974)		
E. spinax	—	52	13	25	36	—	19	0.290	0.287	Holden (1974)		
Ginglymostoma cirratum	—	425	28	7	150	—	30	0.141	0.068	Bigelow and Schroeder (1948)		
Heptranchus perlo	—	137	25	18	100	—	20	0.121	0.201	Tanaka and Mizue (1977)		
Hexanchus griseus	—	482	74	15	421	—	108	0.157	0.167	Ebert (1986a,b)		
Pseudotriakis microdon	—	295	85	29	—	—	2	0.340	0.340	Holden (1974)		
Scoliodon laticaudus	—	74	15	20	35	2	14	—	0.226	Compagno (1984)	0.273	Nair (1976)
Sphyrna tiburo	—	110	32	27	75	—	12	0.318	0.344	Castro (1983)		
S. zygaena	—	396	50	13	220	—	40	0.135	0.135	Castro (1983)		
Triakis barbouri	—	40	10	25	—	—	2	0.288	0.288	Holden (1974)		

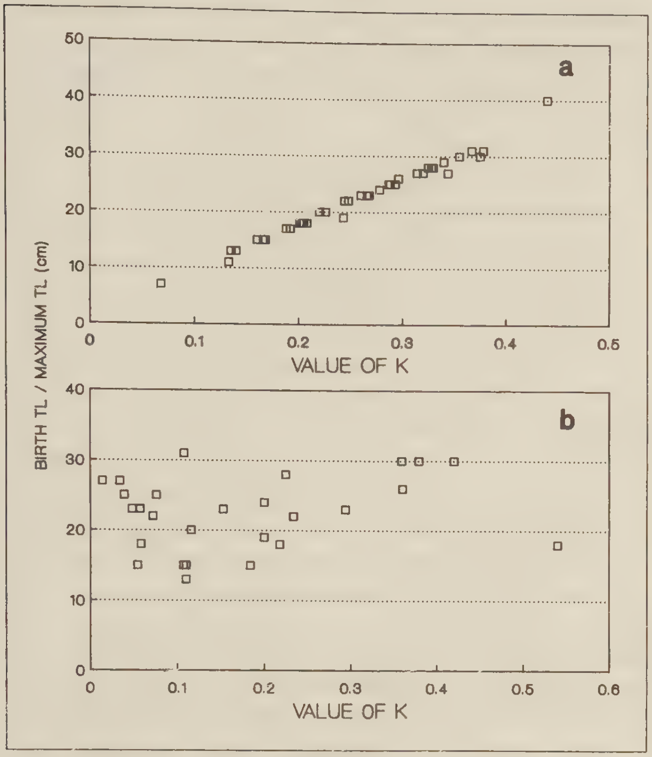

Figure 1.
(a) Ratio of birth size to maximum species size (in cm TL) against predicted *K* value (holden's method, 1974). (b) Ratio of birth size to maximum species size (in cm TL) against empirically-derived *K* value. (From literature.)

Table 3.
Species of sharks with *K* values in agreement with both calculated and empirically derived sources.

Isurus oxyrinchus
Carcharhinus amblyrhynchos
Galeocerdo cuvieri
Galeorhinus japonicus
Mustelus californica
Mustelus manazo
Prionace glauca
Rhizoprionodon terraenovae
Triakis semifasciata
Scoliodon laticaudus
Squalus acanthias

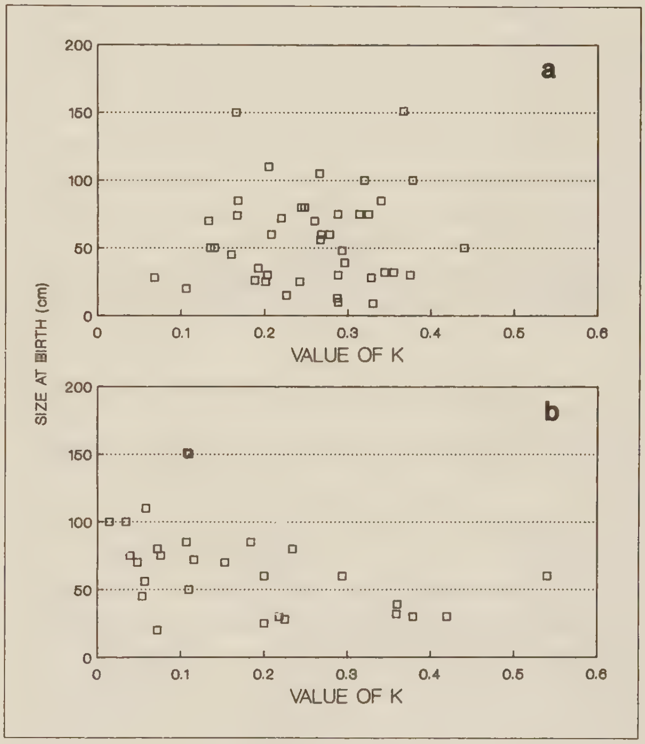

Figure 2.
(a) Size at birth plotted against predicted *K* value (Holden's method). (b) Size at birth plotted against *K* (empirical data).

(Table 2) with calculated and empirically derived *K* values (Table 3). The scatter of plotted points for "Size at Birth vs. *K*" (Figures 2a and 2b) did not support the Holden equation. There is a slight trend for sharks born at a large size to have a smaller *K* value, but there were too many exceptional points for a generalization. The same pattern exists for "Maximum Size vs. *K*" (Figures 3a and 3b), with a trend for larger sharks to have a smaller *K*, and for "Number of Embryos vs. *K*" (Figures 4a and 4b) in that sharks with greater litter sizes usually have a smaller *K* value.

A final cross comparison is made in Figure 5, where calculated *K* values are plotted on the abscissa and empirically derived *K* values are plotted on the ordinate. Points that fall on or near the x = y diagonal line may support Holden's method. There are, however, more points in disagreement. Many of these points are the result of long and careful studies of shark growth and cannot be ignored. Perhaps Equation (3) applies only to certain sharks, in this case, those that fall along the line. Table 3 lists the sharks that graph close to the x = y line of Figure 5. These sharks seem to span the full spectrum of taxonomy, size, mode of reproduction, growth rate, and lifestyle. Their only common denominator may be that their embryonic growth is of the same order as their postpartum growth.

Until more accurate work is available to confirm or refute these findings, Holden's unique method should be employed with caution and verified with each application. Holden intended this method to be a rough guide in the absence of empirical data. These analyses show that the method is too uncertain for general use and may work only

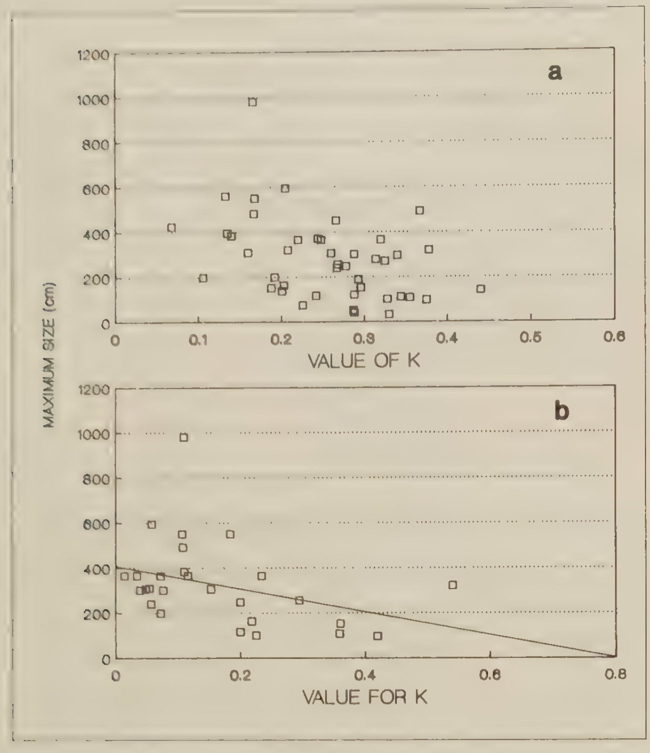

Figure 3.
(a) Maximum size plotted against predicted *K* value (Holden's method). (b) Maximum size plotted against *K* (empirical data).

for a specific and as yet unidentified group of sharks. Empirical data is needed for accurate growth determination.

The Fisheries

Shark fisheries are difficult to manage. The fisheries are usually depleted before the administration of regulatory measures can be effected. Local fisheries managed by artisanal fishermen working a mixed stock of several shark species can be successful and productive indefinitely. Large scale directed fisheries are another matter. There is not enough resilience in even the most fecund and abundant elasmobranchs, the skates and spiny dogfish, to maintain an intensive fishery (Holden 1977). Management practices that could work with sharks, such as limited entry, hook and mesh size limits, catch quotas, seasonal protection of gravid females, and catch restrictions to males, all require extensive management effort, sometimes on an international level. Bedford (1987) has pointed out: "In the real world of economics, politics, special interests, governmental procedures, and rapidly developing fisheries. . . [the shark fishery] is almost surely doomed to failure."

The biological characteristics of a stock of sharks that may support a directed fishery would be one that is naturally abundant, has a fast growth rate (a *K* value of over 0.20),

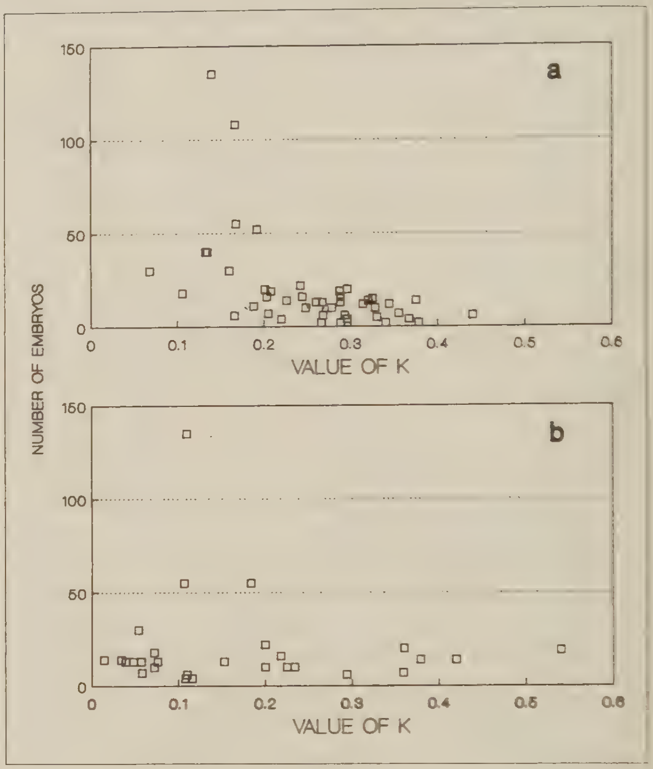

Figure 4.
(a) Number of embryos plotted against *K* value (Holden's method). (b) Number of embryos plotted against *K* (empirical data).

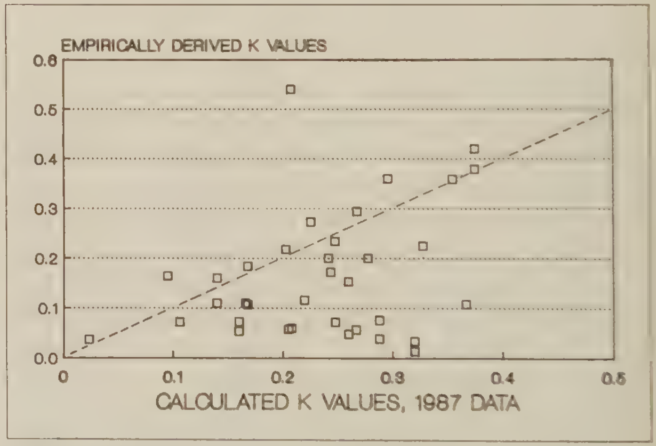

Figure 5.
Comparison of *K* values, calculated vs. empirical values (Holden's method, 1987).

and a relatively high fecundity, regularly producing large numbers of embryos with a fairly short gestation time. In reality, shark fisheries do not originate from a search for a suitable population or target species. They begin because a market develops for a species that becomes accessible owing to a recent gear advancement, collapse of a similar fishery (i.e., swordfish), increased market demand, or the discovery of a latent or burgeoning stock that the market will accept. The California fishery for *Alopias vulpinus* is an example.

California Thresher Shark Fishery

The California pelagic fishery for the common thresher, *Alopias vulpinus*, has been well documented (Cailliet and Bedford 1983; Bedford 1987). The fishery began in 1977 and succeeded because of public acceptance of sharks as table food. The fishery began using drifting gill nets patterned after those used to catch the soupfin shark, *Galeorhinus galeus*, in the 1930s and early 1940s. These surface fishing gillnets also caught a number of swordfish (*Xiphias gladius*). The thresher shark soon became a secondary target for the gillnet fisherman and attempts to manage the catch were confused and compounded by more powerful attempts to manage and limit the swordfish fishery. Bedford (1987) details the case history of legal management action and the rise and fall of the thresher shark fishery. Thresher shark landings peaked in 1982 at 2400 million pounds, by 1987 the catch had dropped to less than 400 million pounds. As an active participant he states: "The dispute we mediated seldom had anything to do with the thresher shark. The control of the swordfish prompted the adoption or abolition of most regulation" (Bedford 1987). After 9 years (in 1986) the limited entry fishery was closed seasonally during prime thresher shark fishing months, June, July, and half of August, to allow stocks to rebuild.

Western Atlantic Porbeagle Fishery

In 1960 a longline fishery for porbeagle sharks, *Lamna nasus*, was established in the western North Atlantic, primarily by the Norwegians. From 1961 to 1964 annual catches increased from 1,800 to 9,300 t, then declined sharply to about 200 t (Casey et al. 1978). Growth to maturity in the porbeagle shark takes 6 to 9 years. Normally, four young are produced (Aasen 1961). The Norwegians were interested enough in porbeagles to send a biologist along on a commercial trip during which 2,488 sharks were caught. He produced a valuable paper on length and growth of the porbeagle (Aasen 1963). After 1964, porbeagles became very scarce. Porbeagles were almost unknown to the U.S. market before 1960. The Faeroese, who received an allocation of 500 t of porbeagle sharks from U.S. waters in 1978, caught only 5 t in 1980 and 100 t in 1982. In 1983 and 1984 they did not fish in the U.S. Fisheries Conservation Zone (FCZ) (Casey and Hoey 1985). Longlining efforts in waters north of Cape Cod by the NMFS Apex Predator Investigation and by cooperating commercial fishermen has yielded very few porbeagle sharks. The directed fishery for porbeagle sharks, so heavily impacted the shark in four seasons of fishing, that the population in the northwest Atlantic apparently still has not recovered to prefishery levels.

Other Fisheries

Between 9,800 and 17,300 t of sharks are landed annually in the U.S. Atlantic FCZ principally from U.S. recreational fishermen and as a bycatch of U.S. and foreign vessels fishing with longline for tunas and swordfish, or trawling for squid and finfish (Anderson 1985). As long as these fisheries remain sporadic, or undirected, they probably will not impact the stocks of pelagic sharks to any great extent. In the last ten years, a directed fishery for sharks has started off the southeast coast of the United States. A reliable market developed for both fins and flesh. From 1979–1985 there was a linear increase in landings which averaged about 290 thousand pounds per year. In 1986, the linear trend turned geometric and increased by 629 thousand pounds. In 1987, landings increased 2.7 million pounds, to a total of 5.3 million pounds (Larry Massey, Operations Research Analyst, NMFS, SEFC, Miami, FL, pers. commun., Nov. 29, 1988.). This fishery may be viable for a time because it draws from a broad base resource—numerous shark species, many of which migrate over a large area of the Atlantic. However, without conservative management practices, history has shown that even durable populations succumb to "recruitment overfishing".

Population Life-History Problems

The shark populations have proven to be largely unresilient in the face of directed fisheries. Certainly the porbeagle populations have taken years to recover. Stock and recruitment are closely linked as there is no annual wellspring of countless progeny with which to rebuild exploited stocks. It remains to be proven if any shark species increase their fecundity as stocks diminish. Shark populations do not seem to be food or resource limited (see Hoenig and Gruber 1990); therefore, density-dependent mortality may not be an important compensatory mechanism. An exception to this may take place in certain reef or lagoon environments (Stevens 1984). There is some evidence for intraspecies predation controlling juvenile abundance. Van der Elst (1979) observed that the population of young dusky sharks off Durban, South Africa, increased with the removal of large predators by the net meshing program.

The sandbar shark, *Carcharhinus plumbeus*; the blacktip, *C. limbatus*; the bonnethead, *Sphyrna tiburo*; and other species of sharks, skates, and rays use coastal and estuarine areas as pupping and nursery areas in the United States. Doubtless, estuarine areas around the world shelter elasmobranch nursery grounds. In industrialized countries these valuable regions are heavily impacted by pollution, encroaching development, overburdening recreational use, and other effects of mankind. Great South Bay, Long Island, was once a nursery for the sandbar shark (Nichols and Murphy 1916). They are no longer caught in this bay. Preservation of natural coastal areas is as important to shark survival as it is to that of their forage and countless other valuable animals.

As ocean ecosystems are impacted by man, concern must be raised for the preservation and maintenance of pupping and nursery areas for sharks. The blue shark, *Prionace glauca*, pups in pelagic waters of the eastern Atlantic (Pratt 1979). Recently one of the authors (Casey) has been delimiting the blue sharks' time and place of parturition. In the advent of an intense fishery for the blue shark, this area should be defined and perhaps closed to fishing during the pupping season.

Conclusion

Sharks, as a group, are not good candidates for large scale directed fisheries. Sharks produce a relatively small number of large young which grow slowly and mature late in life. These factors result in a close relationship between stock and recruitment. Understanding the life-history strategies and mechanisms that limit shark populations will help us define the biological factors that affect shark fisheries. This understanding is not likely to increase the harvest, but it will help us regulate it. With wise management, a steady market may be supplied from some fecund and abundant species.

Other shark species may have suitable population dynamics to support future fisheries. Fishermen's abilities to fish farther offshore, and in deep waters, will develop or expand fisheries in areas where consumers will support a market for them. In light of the expanding demand for marine resources throughout the world, the increased use of sharks is assured. If these fisheries are to be maintained at sustainable levels, our continuing task will be to provide new and precise information on both elasmobranch life-history parameters and the human history of dealing with shark fisheries so that both sharks and man will benefit.

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Classification of Reproductive Modes in Sharks with Comments on Female Reproductive Tissues and Structures

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ABSTRACT

Shark reproductive modes are reclassified based on previous reviews of shark reproduction and systematics with the addition of new material on histology of various reproductive structures. The objectives of this study are 1) to comment on the evolutionary development of viviparity in sharks, 2) to introduce a new classification of reproductive mode in sharks and 3) to report the fine structure of the intrauterine mucosa and placenta from one oviparous and ten viviparous sharks.

The reproductive modes of the species examined are divided into oviparity (*Cephaloscyllium umbratile*) and four types of viviparity. These four viviparous types can be divided into two groups based on whether or not the uterus is compartmentalized.

Introduction

The chondrichthyan fishes, one of the oldest living groups of jawed vertebrates, have evolved considerable reproductive diversity ranging from oviparity to viviparity (Wourms 1977). According to Wourms et al. (1988), oviparity is confined only to the three extant families of chimaera, all four families of skates and 10 of 22 families of sharks. Viviparity is widespread in chondrichthyan fishes (453 of 700 species) and is particularly characteristic of sharks, occurring in 69% of extant species. Sharks are known to exhibit several complex modes of viviparous diversity. Since sharks are generally of less economic importance than many teleosts and are typically difficult to obtain and maintain as experimental animals, little is known about their reproduction (Dodd 1983).

The reproductive modes of chondrichthyan fishes have been reviewed by Amoroso (1960), Breder and Rosen (1966); Hoar (1969); Wourms (1977, 1981); Dodd (1983); and Wourms et al. (1988); and have been categorized in several ways. Wourms (1977) divided chondrichthyan fish reproduction into oviparity and viviparity. He subsequently subdivided viviparity into aplacental and placental viviparity. Aplacental viviparity includes species whose embryos are 1) solely dependent on yolk reserves; 2) oophagous; and 3) have placental analogues. Placentation includes the yolk-sac placenta. Teshima (1981) used a similar nonplacental and placental classification system. He divided nonplacental classification into two categories based on the presence or absence of uterine compartments. Teshima also stated that placentation is further temporally and morphologically divided into two types of placentae: one which is established during midgestation and a second type established soon after implantation. Wourms (1981) further classified chondrichthyan reproduction by trophic relationships between mother and embryo. His two major groups are composed of 1) facultative viviparity and 2) obligate viviparity. Obligate viviparity is subdivided into lecithotrophs and matrotrophs. Matrotrophs include 1) oophagous and adelophagous; 2) placental analogues; and 3) yolk-sac placental species.

Viviparity probably evolved in association with phylogeny. Therefore the classification of reproductive modes may reasonably involve systematics. However, the morphological classifications of Wourms (1977) and Teshima (1981) do not seem to fully reflect systematic relationships because in some cases phyletically related species may differ in reproductive morphology, e.g., nonplacental *Mustelus* (*M. manazo*) versus placental *Mustelus* (*M. griseus*). This results from the initial division of viviparity on the basis of placental establishment. The trophic patterns of Wourms (1981) also do not follow systematic classifications because trophic relationships appear to display a high degree of convergence and parallelism and do not follow phylogenic relationships.

Table 1.
Sharks species and their biological data used in this study.

		Mother			Embryo	
Species	No. of specimens	Total length (cm)	Ovary weight (g)	No. of embryos	Total length (cm)	Body weight (g)
Oviparity						
Cepholoscyllium umbratile	1	100	300	—	—	—
Viviparity						
Lamna ditropis	1	194	5450	4	36.8-39.3	3710-3920
Alopias pelagicus	2	264-282	230-270	4	42.1-52.1	175-250
Squalus mitsukurii	3	93-120	30-120	6	—	—
Orectolobus japonicus	2	107-119	38-44	10-22	20.6-24.5	40-80
Squatina japonica	2	93-98	7-45	8-9	18.5-21.0	90-100
Triakis scyllia	2	113-127	90-150	3-22	14.2-21.5	30-58
Mustelus manazo	7	75-85	13-21	3-6	26.2-29.0	49-72
M. griseus	12	93-107	7-29	8-15	20.4-30.8	31-74
Prionace glauca	11	204-241	75-180	7-27	18.0-40.0	80-210
Scoliodon laticaudus	10	35-54	—	1-10	0.5-15.9	—

Materials and Methods

Pregnant sharks of ten genera were used in the present study. This study included 11 species in 8 families. These are *Cephaloscyllium umbratile*, *Lamna ditropis*, *Alopias pelagicus*, *Squalus mitsukurii*, *Orectolobus japonicus*, *Squatina japonica*, *Triakis scyllia*, *Mustelus manazo*, *M. griseus*, *Prionace glauca*, and *Scoliodon laticaudus*. The biological data for these sharks are shown in Table 1. *L. ditropis*, *A. pelagicus*, and *S. mitsukurii* carried middle-term embryos and the other seven viviparous sharks carried full-term embryos. Most sharks were caught with gill nets, pelagic, or bottom longlines operated by commercial fishing boats or by the research vessel *Tansei Maru* (Ocean Research Institute, University of Tokyo), operating in Japanese waters from 1977 to 1981. *Alopias pelagicus* were captured with a tuna longline from the training vessel *Nagasaki Maru* (University of Nagasaki), in the eastern Indian Ocean. *Scoliodon laticaudus* were obtained from the fish markets of Malacca, Malaysia, and Kanka, Singapore in October, 1978 and in September, 1979 respectively.

The uterus, embryonic yolk sac, and placenta were histologically and histochemically investigated using light and electron microscopes. For light microscopy, tissues were fixed in 10% neutral formalin or Bouin's solution. Sections, 4-10 μm in thickness, were made by the usual paraffin method and stained with haematoxylin—eosin, Azan, and Periodic Acid Schiff (PAS) solutions. For electron microscopy, small pieces of tissues were fixed for several days in a cold fixative containing 2% paraformaldehyde and 2% glutaraldehyde in 0.1M sodium phosphate or containing cacodyrate buffers (pH 7.4) with 10% sucrose added. They were postfixed in 2% osmium tetroxide, dehydrated in graded ethanol, embedded in Epon 812 and made into ultrathin sections with a LKB-ultratome. After double staining with uranyl acetate and lead citrate, the sections were examined with a JEM-100CX electron microscope. Some of the 1 μm sections were stained with toluidine blue for light microscopy observation.

Two experiments were conducted to demonstrate the placental transport of macromolecular weight materials. The first experiment used a trypan blue stain technique to demonstrate placental transport. Three pregnant *M. griseus* (91.3-100.0 cm in TL, carrying near full-term embryos, 20.4-27.5 cm in TL) were injected daily in the caudal vein with 10-15 mL of 0.8% trypan blue in physiological saline. The fishes died one, two, and four days after the injections started. Embryonic tissues were examined to see if the stain reached them.

The second experiment was conducted on six, live, pregnant *M. griseus* (92.5-103.0 cm in TL, carrying near full-term embryos, 24.5-30.8 cm in TL). The pregnant females were injected with a 10-15 mL solution containing 0.1 g/mL of "Horse radish peroxidase" (HRP: Wako Chem. Co.) in the caudal vein. The fishes were killed 10, 40, 60 minutes, 3 hours, and 24 hours after injection, and small pieces of placental tissues were dipped in a cold fixative identical to that used for electron microscopy for 1-3 days. Identification of HRP was performed according to Larsson's procedure (1981). As a control, placenta of sharks injected with physiological saline for elasmobranch fish (Fuhner solution) were prepared 24 hours after administration, following the same procedure described above.

In nine viviparous sharks, *L. ditropis*, *A. pelagicus*, *O. japonicus*, *Squatina japonica*, *T. scyllia*, *M. manazo*, *M. griseus*, *P. glauca*, and *S. laticaudus*, the trophic relationship between mother and embryo (nutritive dependency index; NDI) was estimated from the maximum diameter of ovarian ova and embryo weight. Ovarian ova of those sharks were determined to be mature or near mature, judging from their size and color. The NDI was estimated by using the formula

(Embryonic weight (g)/mature egg diameter (mm)^3) × 10^3.

Results

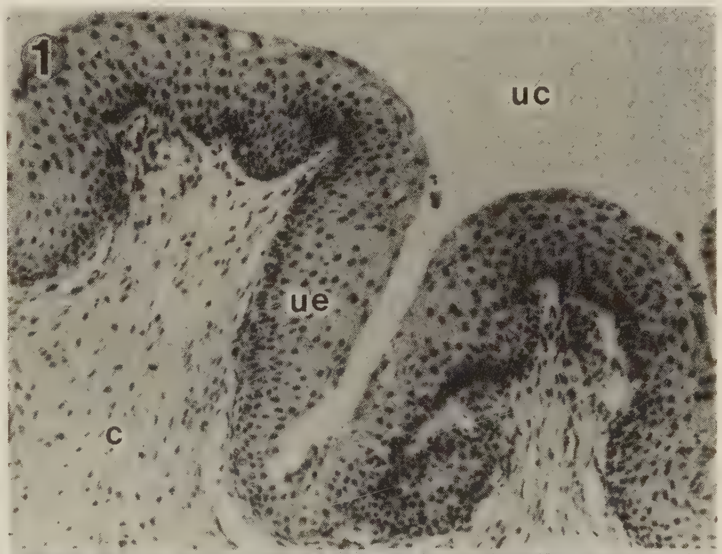
In the following treatment of the histology of the intrauterine epithelium and placenta, the viviparous sharks examined are divided into two basic groups, those with, and those without uterine compartments. Uterine compartments occur in only five families of sharks: Leptochariidae, Triakidae, Hemigaleidae, Carcharhinidae, and Sphyrnidae. All placental species are also included within these families. The development of the uterine compartment is used here to propose a new classification of shark reproductive modes. A provisional classification is shown in Table 2. Viviparity is divided first into two types of uteri—those which do not have uterine compartments and those which do. Those lacking uterine compartments are subdivided into 1) oophagous species and 2) those retaining the yolk sac. Those species with uterine compartments are divided into those that retain the yolk sac and those that are placental species. The results of histological investigation are reported following the order in which these reproductive modes are presented above.

I. The Oviparous Reproductive Mode

The intrauterine mucosa of *Cephaloscyllium umbratile* was composed of stratified epithelial cells (Fig. 1). The juxtaluminal epithelial cells contained PAS positive granules

Table 2.
Reproductive modes of sharks.

I. Oviparity
II. Viviparity
  A. Uterine compartments are not formed
    (1) Type I Uterus - Oophagous
    (2) Type II Uterus - Yolk Sac
  B. Uterine compartments are formed
    (1) Type III Uterus - Yolk Sac
    (2) Type IV Uterus - Placental



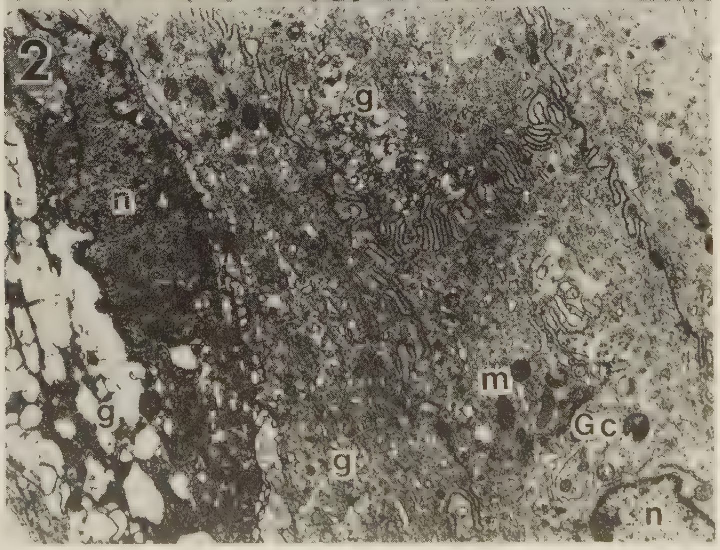
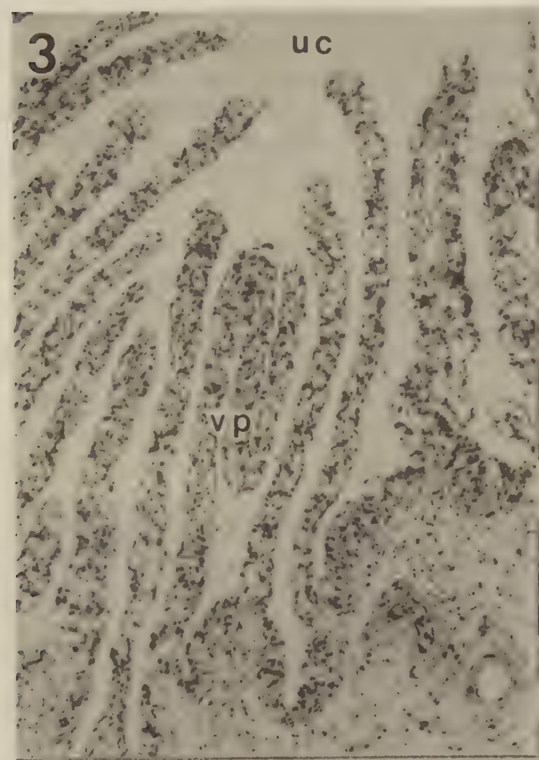


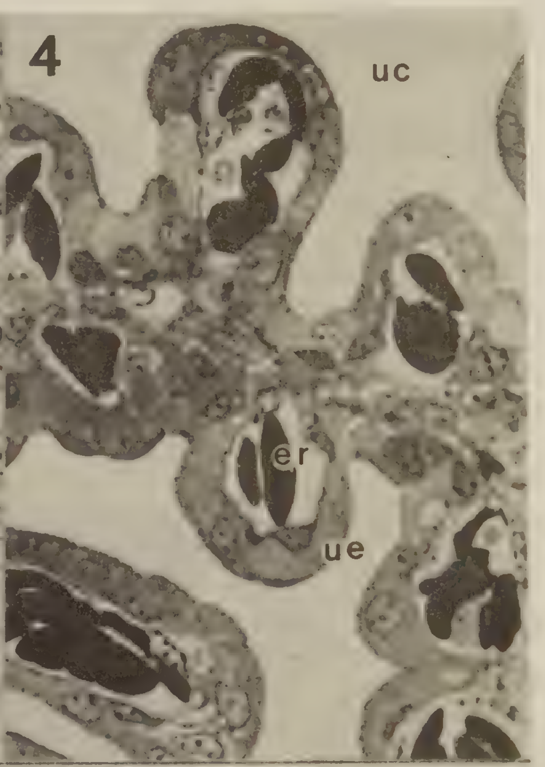
Figure 1.
Intrauterine mucosa of *C. umbratile*. The intrauterine wall is composed of stratified epithelium. H.E. stain. ×25.

Figure 2.
Electronmicrograph of intrauterine epithelium of *C. umbratile*. Granules (g), RER, SER, Golgi complexes (Gc), and mitochondria (m) are present in the cytoplasm. ×4,900.

uc: uterine cavity; ue: uterine epithelium; c: connective tissue; n: nucleus.

in the cytoplasm. A capillary network developed under the epithelium. Many rough and smooth endoplasmic reticulum (RER and SER), Golgi complexes, and numerous oval granules were found throughout the cytoplasm of the epithelial cells in electronmicrograph (Fig. 2), suggesting that the secretory activity of the cell was high.





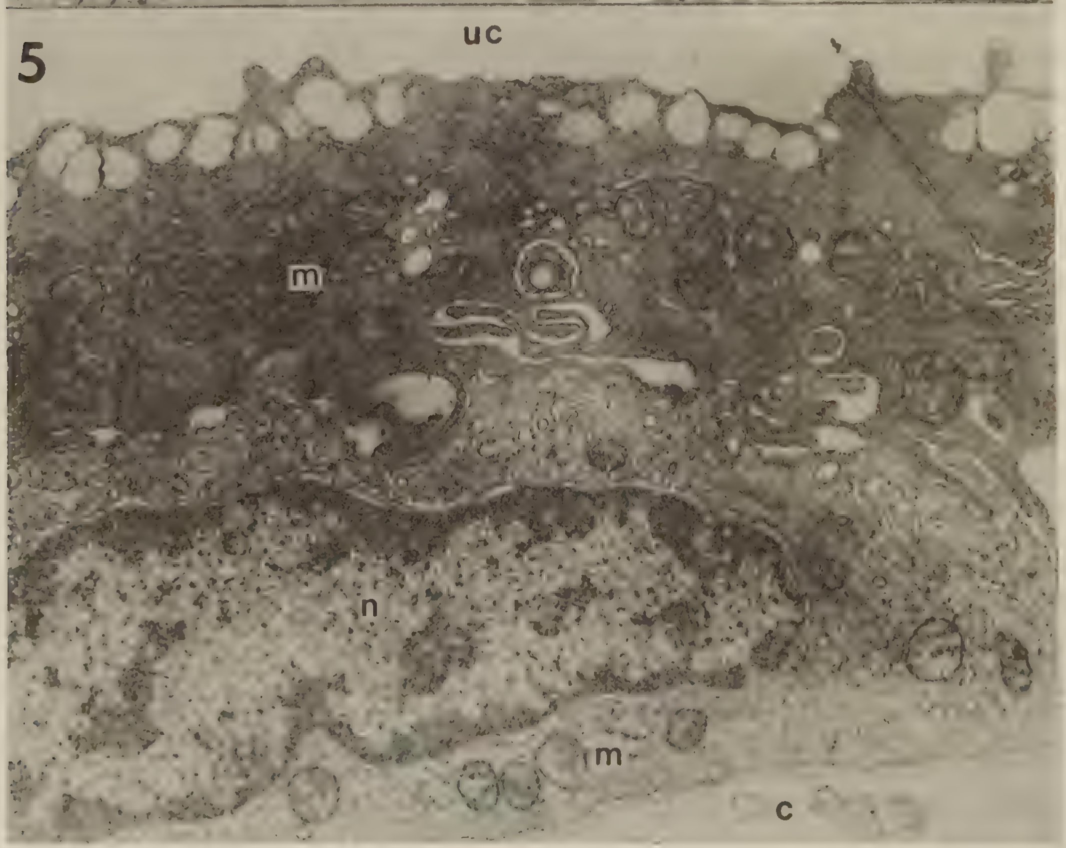


Figure 3.
Intrauterine mucosa of *A. pelagicus*. The mucosa is covered with numerous villiform projections (vp). H.E. stain. ×25.

Figure 4.
Transverse section of intrauterine villiform projection of *A. pelagicus*. The epithelium is composed of two cell layers. The circulatory system is well-developed beneath the epithelium. ×160.

Figure 5.
Electronmicrograph of intrauterine epithelium of *A. pelagicus*. Many mitochondria (m) are present in the cytoplasm. The intercellular spaces are distended. ×18,900.

uc: uterine cavity; ue: uterine epithelium; er: erythrocyte; c: connective tissue; n: nucleus.

II. The Viviparous Reproductive Modes

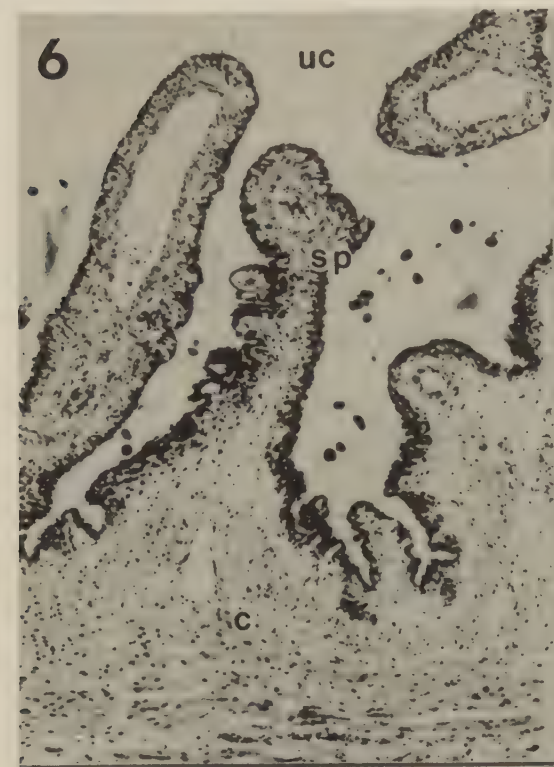
Type I Uterus-Oophagous Species: Species examined which had this type of reproductive anatomy were *Lamna ditropis* and *Alopias pelagicus*. There was fundamentally no difference in the structure of the intrauterine mucosa between these two species. The pregnant intrauterine mucosa was covered with spatulate, villiform projections, 3-5 mm long in *L. ditropis* and 1-2 mm long in *A. pelagicus*, except the anterior one-fifth part of the mucosa, which was covered with deep longitudinal folds (Fig. 3). The mucosal epithelium was composed of two cell layers. Juxtaluminal epithelial cells, were 5-15 μm in height and juxtacapillary cells were extremely flattened (Fig. 4). PAS positive cells were rarely found in the epithelium. A capillary network was close to the epithelium. Electronmicrography revealed that the free surface of the juxtaluminal epithelial cells were rarely covered with short cytoplasmic projections (Fig. 5). Many membrane bounded granules, which were oval in shape, 0.1-0.5 μm in length, lined the apical portion of the cell. The fine structural feature of the granule was similar to that observed in the juxtaluminal epithelial cells of the pregnant uterus of *Squalus acanthias* reported by Jollie and Jollie (1967). Mitochondria, Golgi complexes, and small granules were distributed throughout the cytoplasm. The epithelial cells were joined to adjacent cells by a junction complex in the apical portion of the cell. A few desmosomes were present on the lateral surface. The lateral and basal surfaces of adjoining cells were interdigitated and the intercellular spaces were often distended. These distentions of intraepithelial tissue spaces have been observed in association with active water and solute transport (Kaye et al. 1966; Tormy and Diamond 1967; Bonneville and Weinstock 1970; Greven 1977,1980; Jollie and Jollie 1967; Otake and Mizue 1986). The endothelium of the capillary lay close beneath the epithelium and stromal elements were few in the space between the endothelium and the epithelium. The endothelium was flattened and possessed fenestrations. These structures are probably advantageous in exchanging diffusible materials such as gases, water, and solute, between the capillary blood and the epithelium. The uterine epithelium seems to be involved in respiratory exchange and osmoregulation of the uterine fluid.

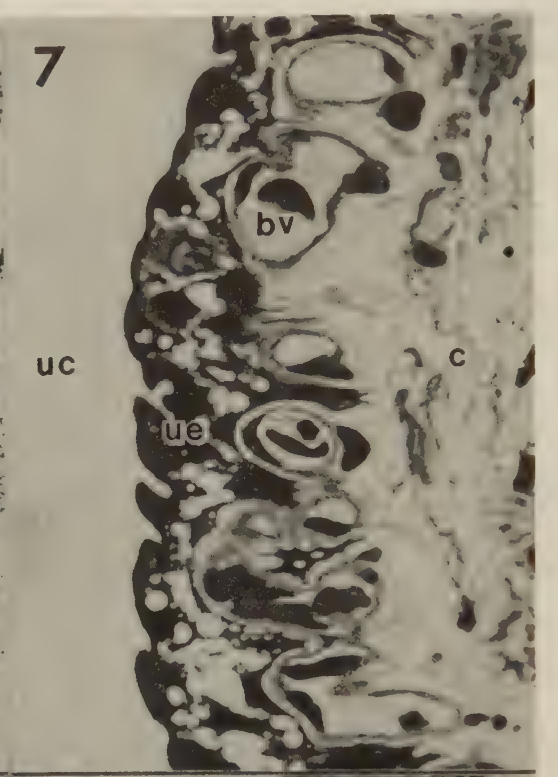
Type II Uterus-Yolk Sac Species: This type includes *Squalus mitsukurii*, *Orectolobus japonicus*, and *Squatina japonica*. In this type, several embryos with attached yolk sacs are contained in each uterus. The morphological aspects of intrauterine mucosa of *S. mitsukurii* were fundamentally the same as that of *S. acanthias* as reported by Jollie and Jollie (1967). The intrauterine mucosa was densely covered with spatular projections, 2-3 mm in length (Fig. 6). The epithelium was composed of two layers of flattened cells (Fig. 7). Juxtaluminal cells were 2-15 μm in height and juxtacapillary cells were 2-5 μm. Just beneath the epithelium lay a well-developed capillary network. In electronmicrography juxtaluminal epithelial cells rarely possessed short cytoplasmic projections on the free surface (Fig. 8). Small light granules were present in the apical portion of each cell. Many mitochondria were distributed in the midbasal portion of the cytoplasm. Intercellular spaces, particularly midbasal spaces, were quite distended. The endothelium of capillaries beneath the epithelium were flattened and possessed many fenestrations. These features are similar to those of *S. acanthias* (Jollie and Jollie 1967) and those of oophagous fishes mentioned above. The epithelium of this species seems to contribute to respiratory exchange and osmoregulation of the uterine fluid.

The intrauterine mucosa of *O. japonicus* possessed numerous villous projections, about 30 mm in length, with branches (Fig. 9). Two or three blood vessels were contained within these villous projections (Fig.10). The epithelium covering the villous projections was composed of two quite flattened cell layers, 2-8 μm in height. Electronmicrography revealed that relatively few cell organella were contained in the epithelial cells and interepithelial spaces were distended (Fig. 11). This feature is similar to that of oophagous fishes and to *S. mitsukurii*, and suggests that the epithelium is involved in respiratory exchange and osmoregulation of the uterine fluid. In contrast, the uterine epithelium between the villous projections was composed of 3-4 layers of epithelial cells (Fig. 9). The juxtaluminal cells were 10-30 μm in height and juxtacapillary cells were 7-10 μm. PAS positive cells were scarcely distributed in the epithelium of this portion. A capillary network was present beneath the epithelium. The connective tissue under the epithelium contained a large amount of tissue fluid suggesting active epithelial secretions. In electronmicrography juxtaluminal epithelial cells between the villi possessed Golgi complexes, mitochondria, and small granules containing low electron dense material in the cytoplasm (Fig. 12). Developed RER was distributed in latero- and infranuclear portions of the cell. They formed cisterna and contained moderately electron dense material in the expanded ends. These features indicate that the cell is actively secretive.

The intrauterine mucosa of *S. japonica* was without projections, differing from the mucosa of the other two species of this reproductive mode. The epithelium was composed of stratified cells whose morphological features were quite similar to that of the oviparous shark, *C. umbratile* mentioned above (Fig. 13).

Type III Uterus-Yolk Sac Species: *Triakis scyllia* and *Mustelus manazo* are included in this reproductive mode. In this type, embryos are contained in membrane-like egg capsules and separated by uterine compartments. The egg capsules are closely attached to the intrauterine mucosal surface. The morphological features of the embryos are similar to those of type II uterus species.





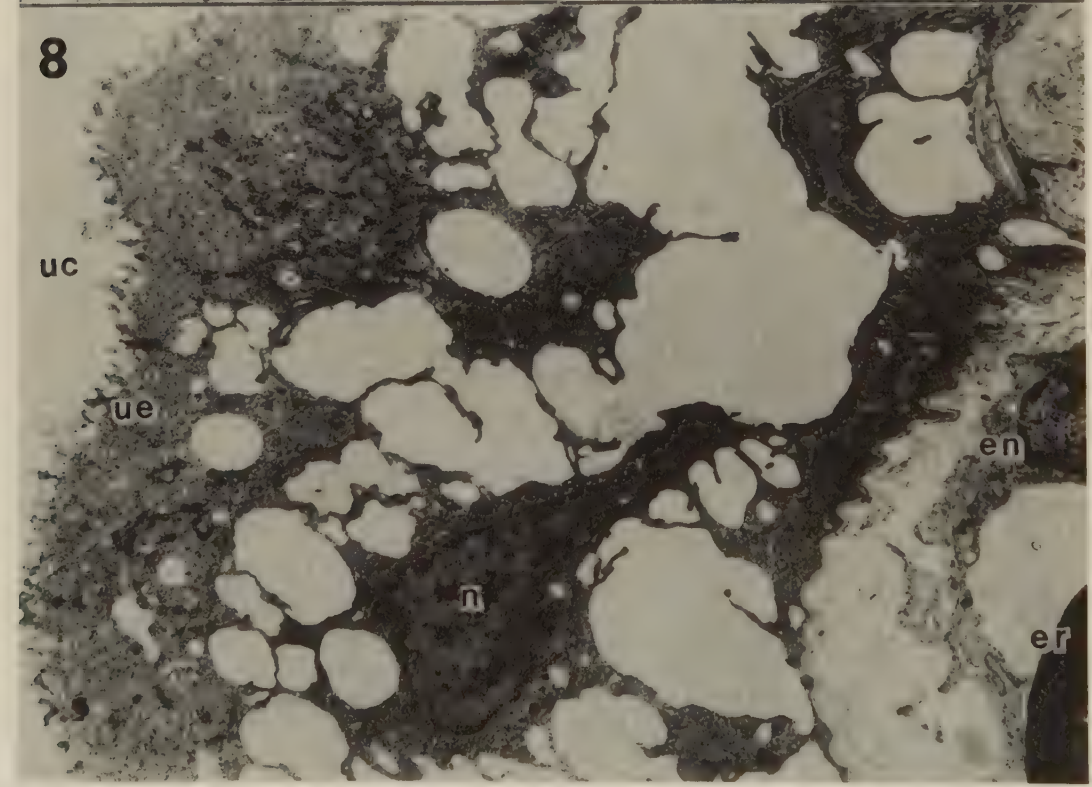


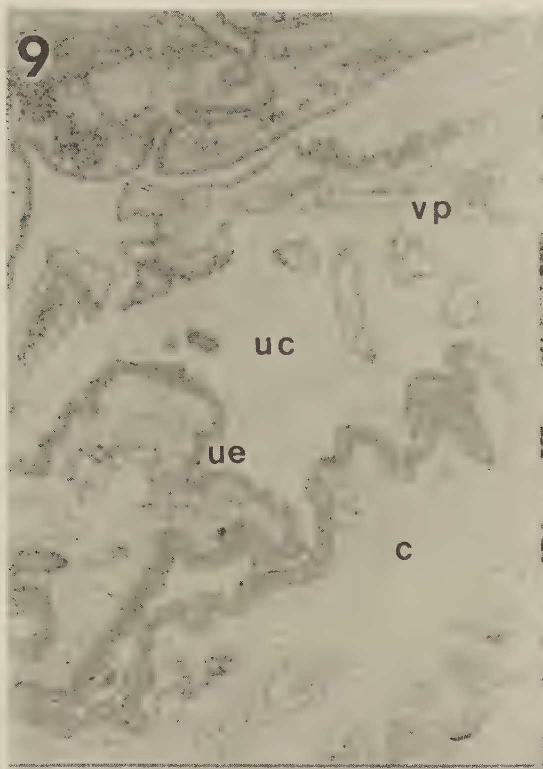
Figure 6.
Intrauterine mucosa of *S. mitsukurii*. The mucosa is covered with spatular projections. H.E. stain. × 25.

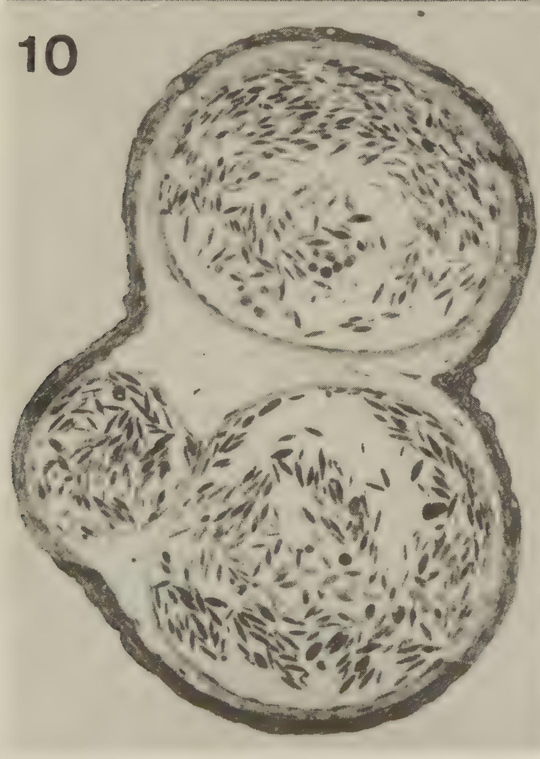
Figure 7.
Intrauterine epithelium of *S. mitsukurii*. The epithelium is composed of two cell layers. The capillary network is well-developed beneath the epithelium. Toluidine blue stain. × 180.

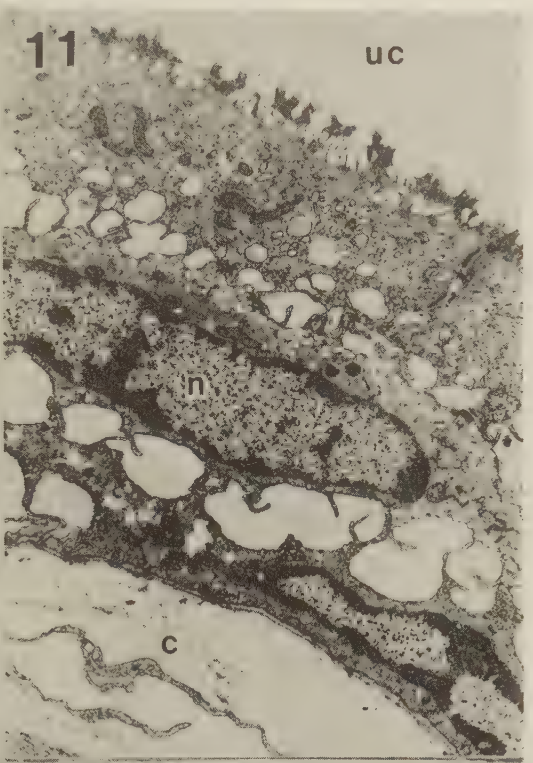
Figure 8.
Electronmicrograph of the intrauterine epithelium of *S. mitsukurii*. Intercellular spaces are quite distended. The endothelium of capillaries (en) lies closely beneath the epithelium. × 5,100.

uc: uterine cavity; sp: spatular projection; ue: uterine epithelium; bv: blood vessel; c: connective tissue; er: erythrocyte; n: nucleus.

The intrauterine mucosal structure was almost the same between *T. scyllia* and *M. manazo*, although the secretive activity of the latter appeared to be higher than the former. The intrauterine epithelium of both species was composed of two layers of epithelial cells (Fig. 14). Mucous cells were distributed in the epithelium. Juxtaluminal epithelial cells were tall, 15–23 μm in height in *T. scyllia* and about 50 μm in *M. manazo*. The cytoplasm stained strongly with







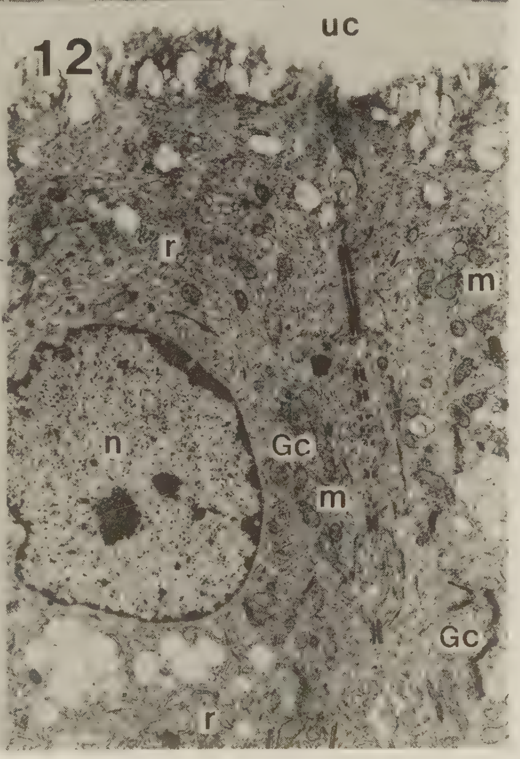


Figure 9.
Intrauterine mucosa of *O. japonicus*. The mucosa is covered with numerous villiform projections. Connective tissue contains copious amounts of tissue fluid. H.E. stain. × 10.

Figure 10.
Transverse section of the intrauterine villus of *O. japonicus*. The epithelium is composed of two cell layers. Three blood vessels are seen within the villus. Toluidine blue stain. × 80.

Figure 11.
Electronmicrograph of the epithelium of villus. The epithelium is composed of two layers of flattened cells. The intercellular spaces are distended. × 2,160.

Figure 12.
Electronmicrograph of the intrauterine epithelium. Developed RER (r), Golgi complexes (Gc), and mitochondria (m) are seen in the cytoplasm. × 4,750.

uc: uterine cavity; vp: villiform projection; ue: uterine epithelium; c: connective tissue; n: nucleus.

PAS. Juxtacapillary epithelial cells had reduced cytoplasm and were 1–8 μm in height in *T. scyllia* and 5 μm in *M. manazo*. Beneath the epithelium was a well-developed capillary network. The connective tissue under the capillaries contained copious amounts of tissue fluid. In electronmicrograph of *T. scyllia* juxtaluminal epithelial cells contained lipid droplets and numerous granules which included low electron dense material. Developed RER and mitochondria were present throughout the cytoplasm (Fig. 15). The lateral and basal surfaces of the juxtacapillary cells

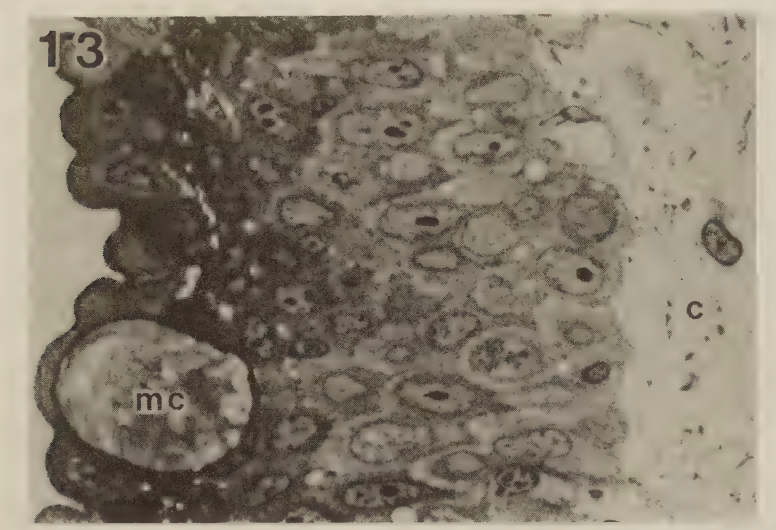
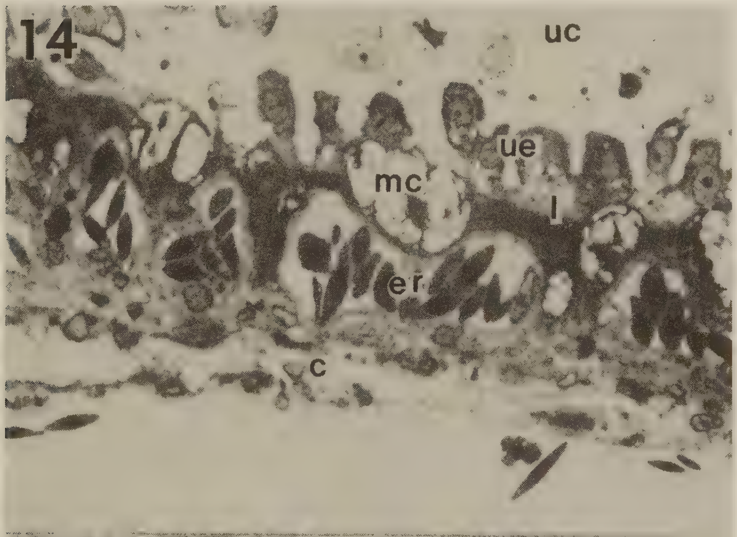


Figure 13.
Intrauterine mucosa of *S. japonica* showing stratified epithelium. Mucous cells (mc) are seen in the epithelium. Toluidine blue stain. × 160.

c: connective tissue.



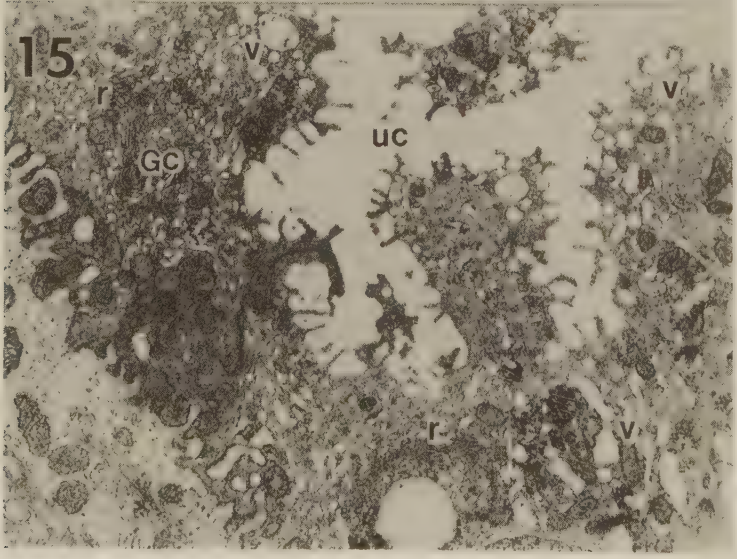


Figure 14.
Intrauterine mucosa of *T. scyllia*. The epithelium is composed of two cell layers and a mucous cell (mc) lining. Epithelial cells contain granules and lipid droplets (l). A capillary network is well developed beneath the epithelium. Toluidine blue stain. × 130.

Figure 15.
Electronmicrograph of intrauterine epithelium of *T. scyllia*. Many vacuoles (v), developed RER (r), and Golgi complexes (Gc) are seen in the cytoplasm. × 8,800.

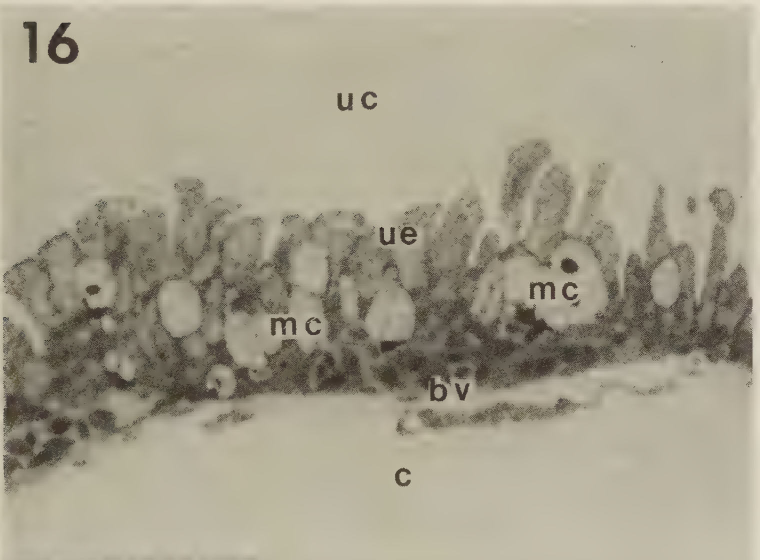
uc: uterine cavity; ue: uterine epithelium; c: connective tissue; er: erythrocyte.

possessed developed cytoplasmic projections. The endothelium of capillaries beneath the epithelium was flattened and possessed many fenestrations. These structures indicate that the epithelium is involved in active secretion of embryonic nutrients in this species. In this group, the uterine fluid seems to contribute more to the embryonic nutrition when compared to type I and type II uteri.

Type IV Uterus–Placental Species: *Mustelus griseus*, *Prionace glauca*, and *Scoliodon laticaudus* are included in this type. In this type the embryos are contained in egg capsules in early gestation or throughout the gestation period (Mahadevan 1940; Senta and Sarangdhar 1948; Gilbert and Schlernitzauer 1966; Schlernitzauer and Gilbert 1966; Graham 1967; Teshima and Mizue 1972; Teshima 1975; Teshima et al. 1978; Otake and Mizue 1985; Hamlett et al. 1985 a,b,c). Each embryo is compartmentalized similar to the type III uterus–yolk sac embryos.

Intrauterine epithelial and placental structures differed among these species. The intrauterine epithelium of *M. griseus*, which did not contribute to placental formation was structurally the same as that of *M. manazo*–type III uterus (Fig. 16), although the secretive activity of the intrauterine epithelium was much higher than that of *M. manazo*. In electronmicrographs, numerous granules were accumulated in the supranuclear portion of the cytoplasm and were seen to discharge their contents into the intrauterine cavity, suggesting high epithelial secretory activity (Fig. 17). The granules varied in shape, size and electron density.

The placenta of *M. griseus* consisted of maternal (intrauterine wall) and embryonic portions (yolk-sac wall), and an egg membrane (egg capsule) as reported by Teshima (1975, 1981) (Fig. 18). The maternal epithelium of the placenta was composed of two layers of extremely reduced cells. Juxtaembryonic cells were 1–8 μm in height. The underlying cells were greatly degenerated in cytoplasm and



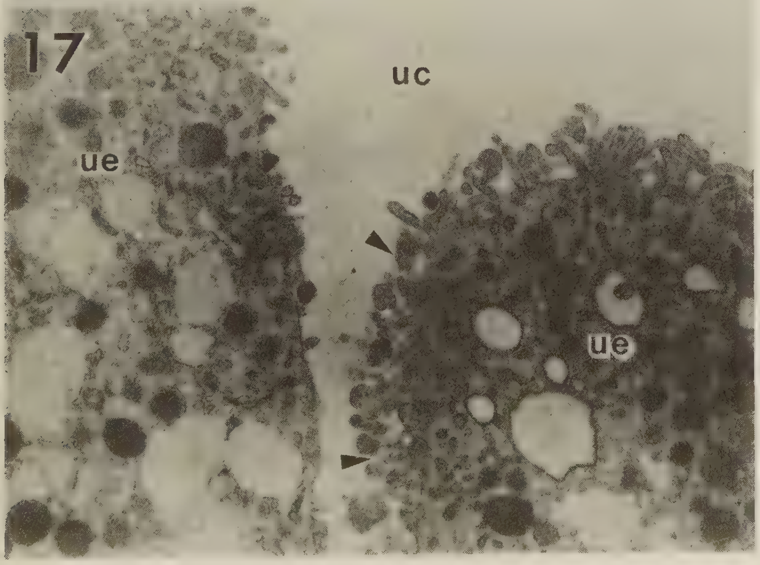


Figure 16.
Intrauterine mucosa of *M. griseus* showing the lining actively secreting cells. Mucous cells (mc) are distributed in the epithelium. Toluidine blue stain. × 80.

Figure 17.
Electronmicrograph of supranuclear portion of the intrauterine epithelial cell of *M. griseus*. Numerous granules with various size and electron density are seen in the cytoplasm. Some granules are seen to discharge their contents (arrowheads). × 18,700.

uc: uterine cavity; ue: uterine epithelium; bv: blood vessel; c: connective tissue.

not identifiable except for the nuclear portion. A well-developed capillary network was found under the epithelium. In electronmicrography the maternal epithelial cells were quite degenerated and cell organella were scarce (Fig. 19). Teshima (1975, 1981) reported that the maternal epithelium of the placenta disappeared and the capillary network underlying the epithelium directly contacted the egg capsule when the embryo grew to more than 150 mm in length. However, in this study of fine structure the maternal epithelium was observed, although it was extremely degenerated, in near full-term gestation. The endothelium of capillaries was located just beneath the epithelium. Stromal elements were not present in the space between the epithelium and endothelium. The endothelium had reduced cytoplasm and many fenestrations.

The embryonic placenta was composed of two layers of flattened epithelial cells (Fig. 18). Juxtamaternal epithelial cells were 1–3 μm in height. Underlying cells were greatly reduced in cytoplasm and were found only in the nuclear portion in light microscopy. A capillary network was present just beneath the epithelium. In electronmicrography, juxtamaternal epithelial cells possessed many cytoplasmic projections in the free surface facing the egg capsule (Fig. 19). Cell organella such as mitochondria, Golgi complexes, and invaginated vacuoles did not occur in the cytoplasm of the epithelial cells, suggesting that the absorption of macromolecular substances did not occur. The intercellular spaces were distended. The endothelium of the capillaries was attached to the basal membrane of the epithelium. The cytoplasm was extremely reduced and fenestration occurred. These structural characteristics of the maternal and embryonic tissues indicate that placental transport is restricted to gaseous and water-solute transport in *M. griseus*.

In *P. glauca* the intrauterine epithelium was composed of two layers of nonsecreting epithelial cells. Juxtaluminal

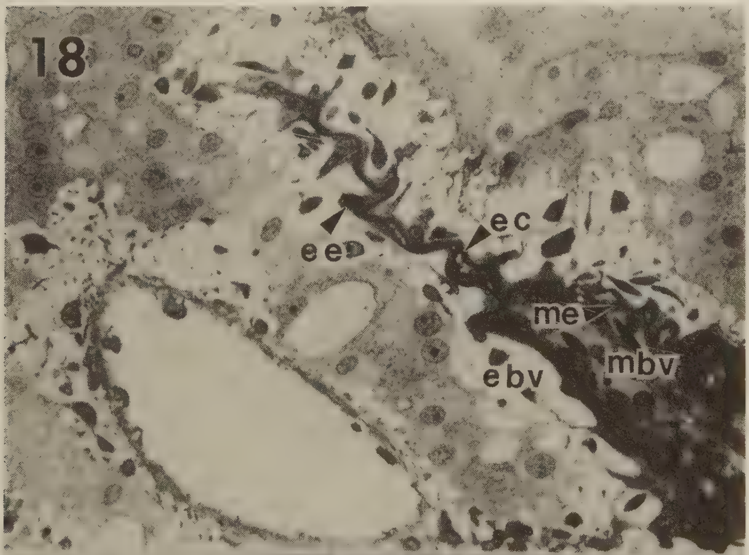


Figure 18.
Placenta of *M. griseus*. Maternal (me) and embryonic epithelia (ee) are flattened and maternal (mbv) and embryonic (ebv) capillary networks are closely located. The egg capsule (ec) is between the two epithelia. Toluidine blue stain. × 80.

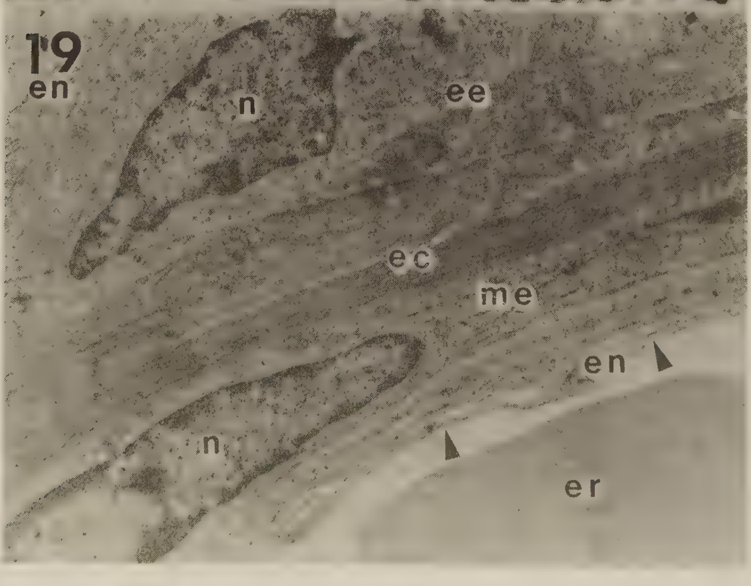
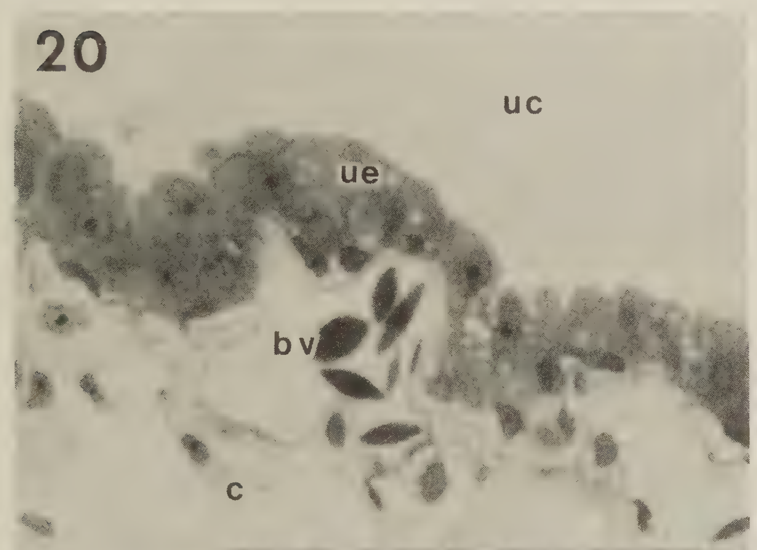


Figure 19.
Electronmicrograph of the placenta of *M. griseus*. Maternal (me) and embryonic (ee) epithelia are quite degenerated. Endothelium (en) of capillaries are quite flattened and fenestrations (arrowheads) are present. × 8,200.

epithelial cells were 10–35 μm in height and underlying cells were flattened (Fig. 20). Just beneath the epithelium was a lining of capillaries. In electronmicrography the free surface of juxtaluminal epithelial cells were rarely covered with microvilli and the surfaces between the villi were coated with invaginations (Fig. 21). Numerous mitochondria were distributed in the basal and lateral portions of the cytoplasm. The intercellular spaces were distended. The capillary endothelium was flattened and few stromal elements were present in the space between the epithelium and endothelium. These features indicate that the epithelium is involved in water and solute transport and plays an important role in the osmoregulation of the uterine fluid.

The placental structure of *P. glauca* is different from that of *M. griseus*. In *P. glauca* the egg capsule degenerated in the placental tissue and the maternal and embryonic epithelia met without any tissue elements (Fig. 22). The epithelium of the maternal placenta was composed of simple, tall, columnar cells, 5–50 μm in height. In the cytoplasm many PAS positive or negative granules and lipid droplets were present. In electronmicrographs, many granules were found in the supranuclear portion of the columnar cells (Fig. 23, 24). Granule inclusions were seen to be discharged into the space between maternal and embryonic epithelia (Fig. 25). RER were mostly distributed in the infranuclear portion, and Golgi complexes were present in the supranuclear portion of the cytoplasm. These structural aspects indicate that the maternal placental epithelium is active in the secretion of macromolecular weight materials. Lateral surfaces of the maternal epithelial cells were smooth and the intercellular space was not distended. The capillaries lay closely beneath the epithelium.

The epithelium of the embryonic placenta consisted of two cell layers (Fig. 22). It was composed of a giant cell, 50–70 μm in height and 75–100 μm in width, and an underlying flattened cell, less than 5 μm in height. The giant cell possessed one or two large irregularly shaped nuclei and granules distributed in the supranuclear portion.



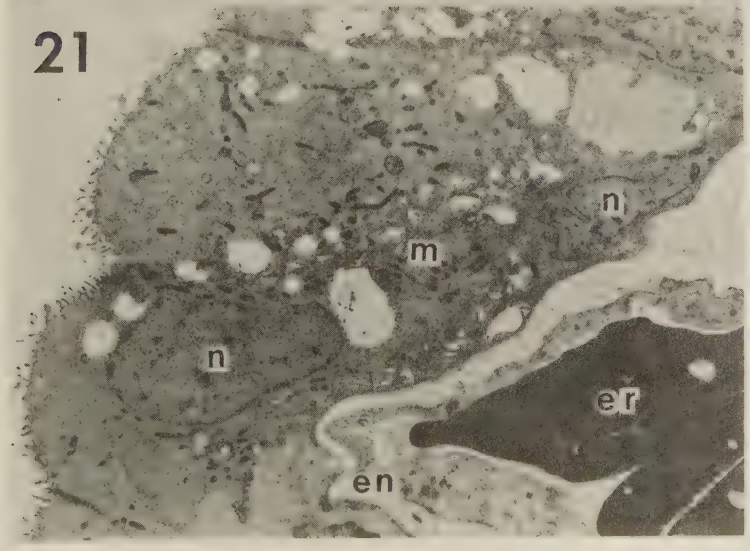
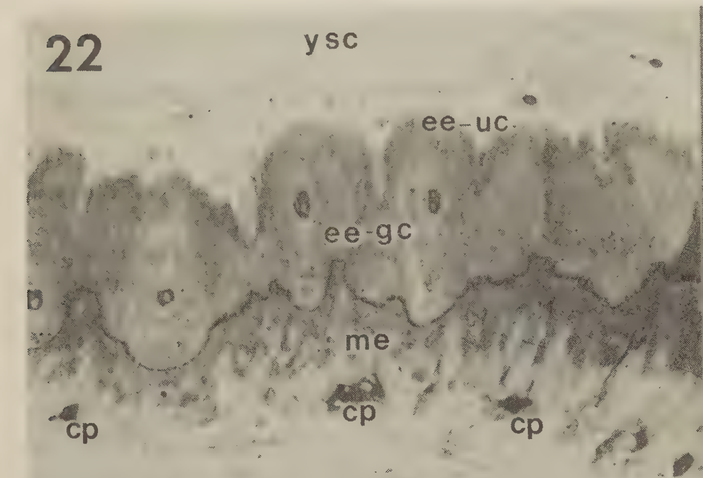
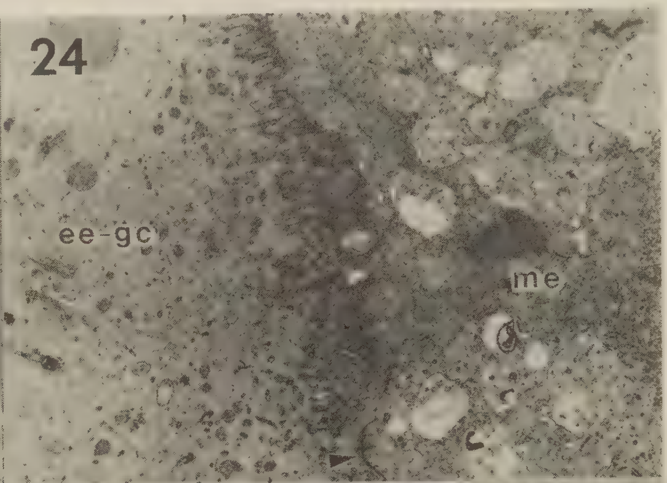


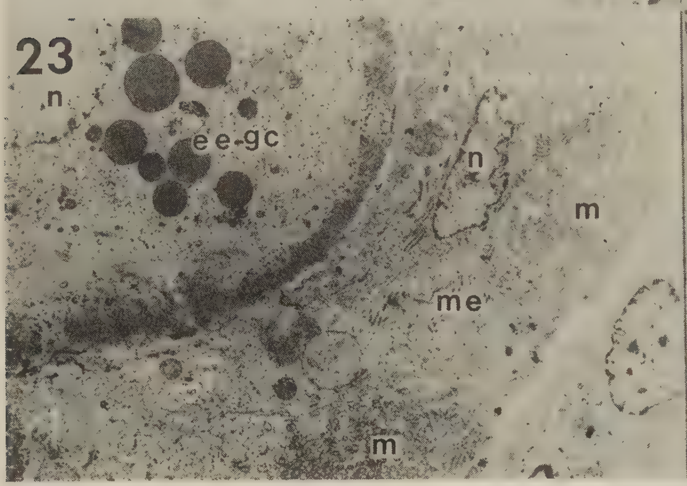
Figure 20.
Intrauterine mucosa of *P. glauca*. The epithelium (ue) is composed of two cell layers. A capillary network beneath the epithelium is developed. Toluidine blue stain. × 270.

Figure 21.
Electronmicrograph of the intrauterine epithelium of *P. glauca*. Epithelial cells are flattened and intercellular spaces are distended. mitochondria (m) are seen in the basal and lateral portions of the cytoplasm. Endothelium of capillaries (en) are located closely beneath the epithelium. × 2,900.

ue: uterine epithelium; bv: blood vessel; c: connective tissue; er: erythrocyte; n: nucleus [from Otake and Mizue (1986)].







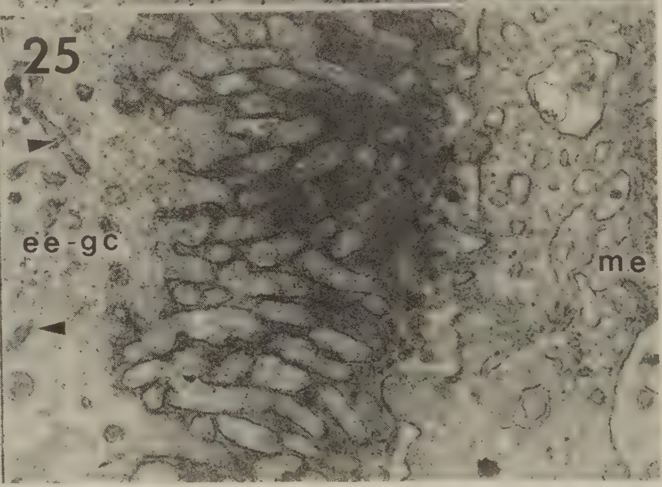


Figure 22.
Placenta of *P. glauca*. Maternal epithelium (me) and embryonic (ee-gc) epithelia are composed of quite active cells. The egg capsule is not present between the maternal and embryonic epithelia. Toluidine blue stain. × 110.

Figure 23.
Electronmicrograph of the placenta of *P. glauca*. Maternal epithelium (me) is composed of simple columnar cells. The maternal epithelial cells contain numerous granules in the supranuclear portion of the cell and mitochondria in basal portion. The embryonic epithelial cell—a giant cell (ee-gc)—contains granules in the supranuclear portion. × 2,350.

Figure 24.
Electronmicrograph of the connecting portion of the placenta of *P. glauca*. The free surface of the embryonic giant cell is mostly covered with microvilli. In some parts it is smooth and in close contact with the maternal surface (arrowheads). × 8,900.

Figure 25.
Electronmicrograph of the space between maternal (me) and embryonic (ee-gc) epithelia of the placenta of *P. glauca*. Numerous electron dense materials are seen in the space. Tubular structure (arrowheads) and coated vesicles are present in the apical portion of the embryonic epithelial cell. × 19,800.

ee-uc: embryonic epithelium - underlying cell; ysc: yolk sac cavity; cp: capillary; m: mitochondria; n: nucleus [from Otake and Mizue (1985)].

Electronmicrographs showed that the free surface of the giant cell was covered with numerous microvilli, except for the portion closely attached to the maternal epithelium (Fig. 23, 24, 25). Tubular invaginations and coated vesicles which suggest absorption of macromolecular weight materials were present in the apical portion of the cytoplasm (Fig. 25). Mitochondria were abundant in the basal portion of the cell, and RER and SER were scattered throughout the cytoplasm. The capillary endothelium lay closely beneath the epithelium, only separated by a basal membrane. The structural aspects of maternal and embryonic epithelia of the placenta indicate that the placental transfer of embryonic nutrients is an active system in *P. glauca*.

The intrauterine wall of Scoliodon laticaudus was covered with a simple epithelium composed of 15–20 μm tall epithelial cells (Fig. 26). Capillaries developed beneath the epithelium. The connective tissue under the capillary network contained large amounts of tissue fluid. Its presence suggests high uterine epithelial secretive activity.

In the *Scoliodon* placenta the egg capsule degenerates in early stages of gestation. The maternal placenta establishes a characteristic trophonematous cup as reported by Mahadevan (1940), Senta and Sarangdhar (1948) and Teshima et al. (1978) (Fig. 27). The surface of the columnar portion of the trophonematous cup was rough and covered with 2–3 layers of epithelial cells. A capillary network developed under the epithelium. The portion of the attach

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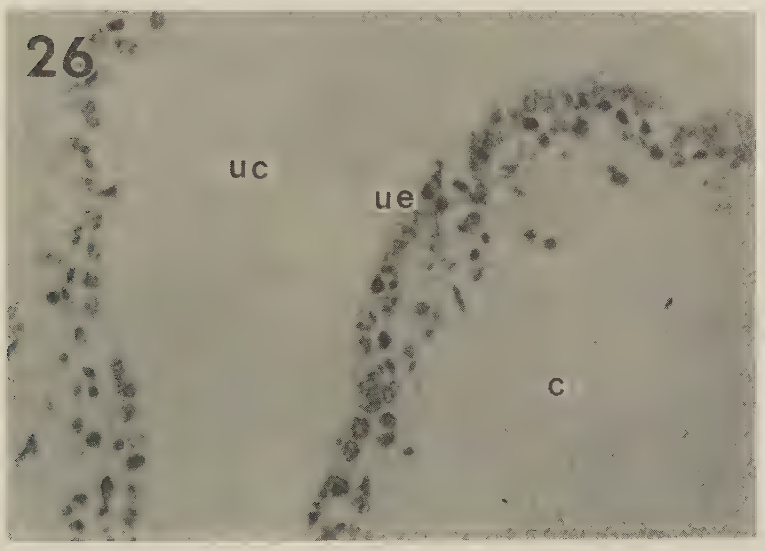

Figure 26.
Intrauterine mucosa of *S. laticaudus*. The connective tissue contains copious amounts of tissue fluid. H.E. stain. × 130.

uc: uterine cavity; ue: uterine epithelium; c: connective tissue.

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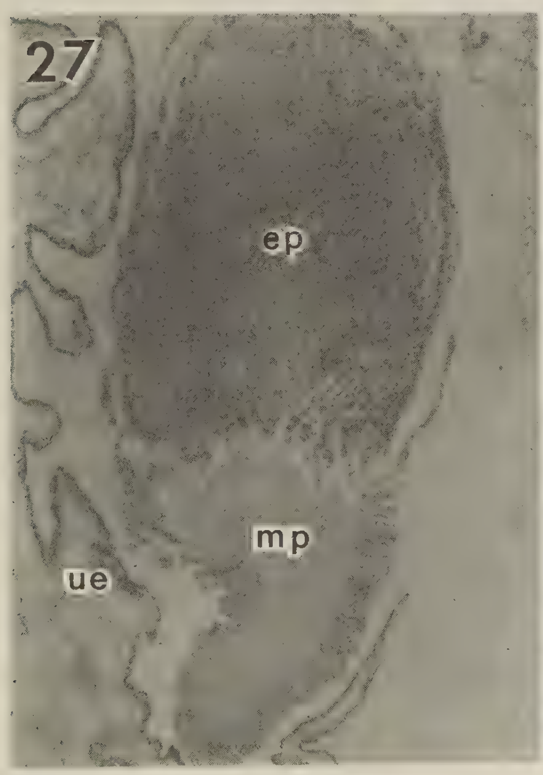

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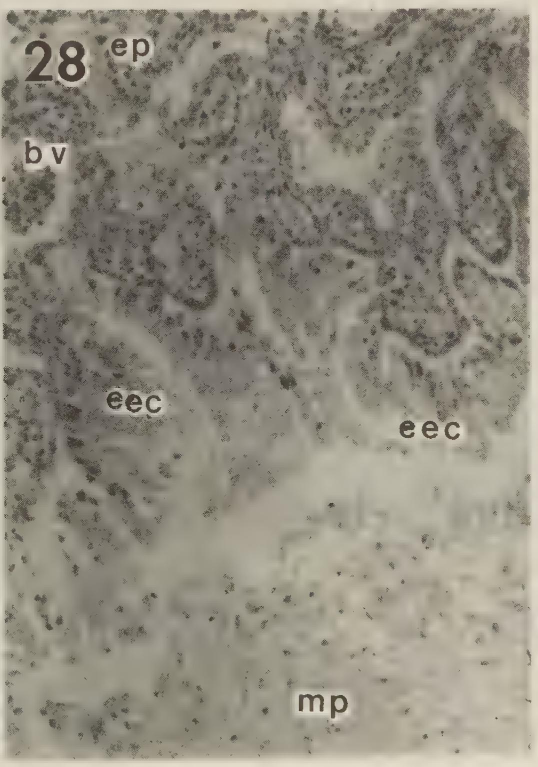


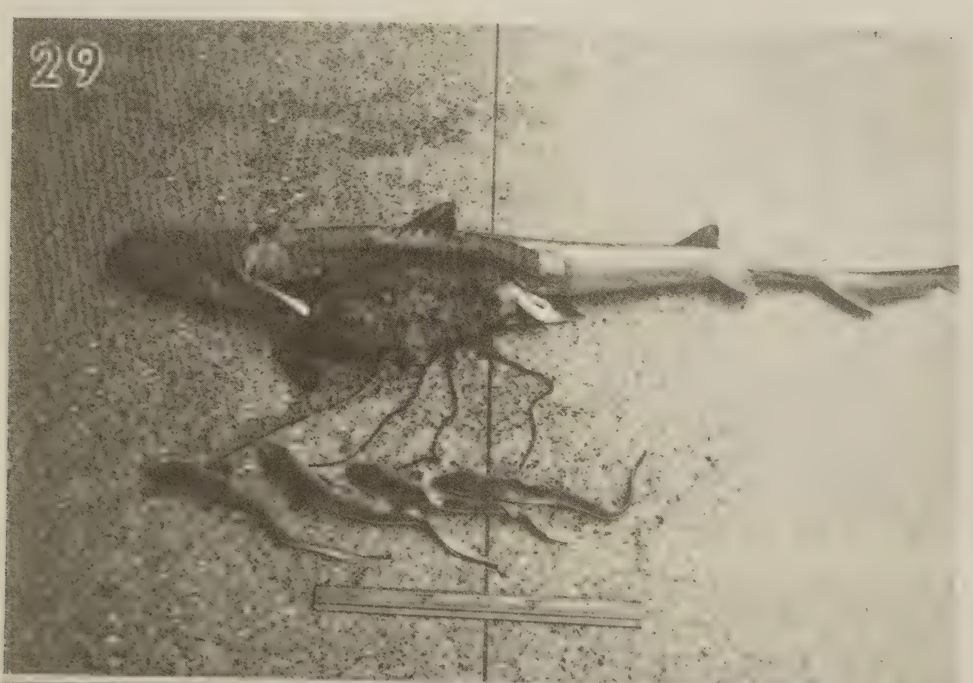
Figure 27.
Transverse section of placenta of *S. laticaudus*. H.E. stain. × 5.

Figure 28.
The placental region where embryonic placenta (ep) contacts the maternal (mp). The maternal epithelium disappeared. H.E. stain. × 50.

ue: uterine epithelium; eec: embryonic epithelial cell.

ment site of the trophonematous cup did not have an epithelium. In this portion, maternal connective tissue directly contacted the embryonic epithelium as reported by Teshima (1981) (Fig. 28).

The embryonic placenta was ovoid in shape and was covered with 1–2 layers of epithelial cells. The epithelial cells were taller in the portion contacting the maternal placenta than those of the portion exposed to the uterine fluid. Within the embryonic placenta, blood vessels were packed and the yolk-sac cavity had completely disappeared: this is in marked contrast to the placentae of *Mustelus*, *Sphyrna*, *Carcharhinus*, and *Prionace*. In these latter genera the yolk-sac cavity connects to the embryonic intestinal lumen by a vitello intestinal duct (Graham 1967; Gilbert and Schlernitzauer 1966; Schlernitzauer and Gilbert 1966; Teshima 1975; Otake and Mizue 1985). Furthermore the vitello intestinal duct degenerates and only a pair of arteries and veins are contained in the umbilical stalk of the *Scoliodon* embryo (Mahadevan 1940; Teshima et al. 1978). These observations suggest that a haemotrophical nutrition transport system similar to the mammalian placenta, might be established in *Scoliodon*. The *Scoliodon* placenta can be



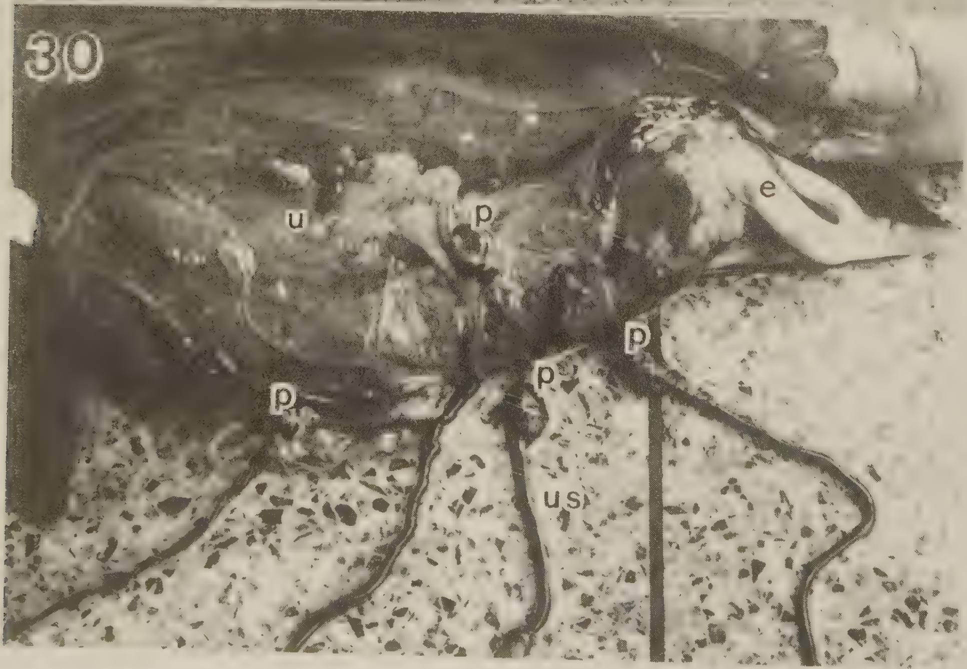


Figure 29.
A pregnant specimen of *M. griseus* administered trypan blue for three days and embryos. The mother is stained completely blue, the embryos are not stained.

Figure 30.
Placenta and embryos of *M. griseus* administered trypan blue for three days illustrating that the embryonic portion of the placentae and embryos are not stained.

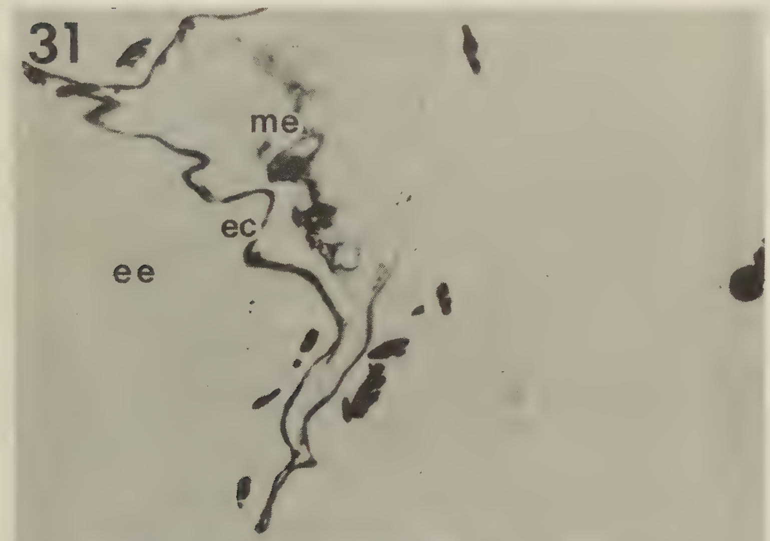
p: placenta; us: umbilical stalk; u: uterus; e: embryo.

said to be more specialized than the other placentae of *Mustelus* (Graham 1967; Teshima 1975), *Prionace* (Otake and Mizue 1985), *Carcharhinus* (Gilbert and Schlernitzauer 1966; Hamlett et al., 1985 a,b,c), and *Sphyrna* (Schlernitzauer and Gilbert 1966).

III. The Nutrient Transport Route in the Placental Shark (*M. griseus*)

Results of the tracer experiment, in which trypan blue was injected into the maternal blood system of pregnant sharks, showed that sharks administered for three days had muscles and internal organs that were strongly stained blue. The embryos and embryonic portion of the placenta were not stained (Fig. 29, 30). This indicates that trypan blue (MW 961) is not transported from mother to embryo through the placental tissue and uterine secretion or is transported in quantities too small to stain embryonic tissues.

A tracer experiment using HRP as a protein marker, which was injected into the maternal blood system, revealed a reaction product of HRP detectable in the maternal blood vessels of the placenta of a shark killed 10 minutes after injection (Fig. 31). In the shark sacrificed 40 minutes after the injection, the reaction product was found only in the maternal tissue of the placenta and egg capsule and not in the embryonic tissue. The reaction product was not detectable in embryonic tissues after 3-h and 24-h administrations of HRP under light microscopy. A search using electronmicrography revealed that the reaction product of HRP was found in granules contained in the epithelial cells of the maternal placenta, egg capsule, and the surface invaginations of embryonic epithelial cells in 40-min, 3-h, and 24-h administered sharks. The reaction product could



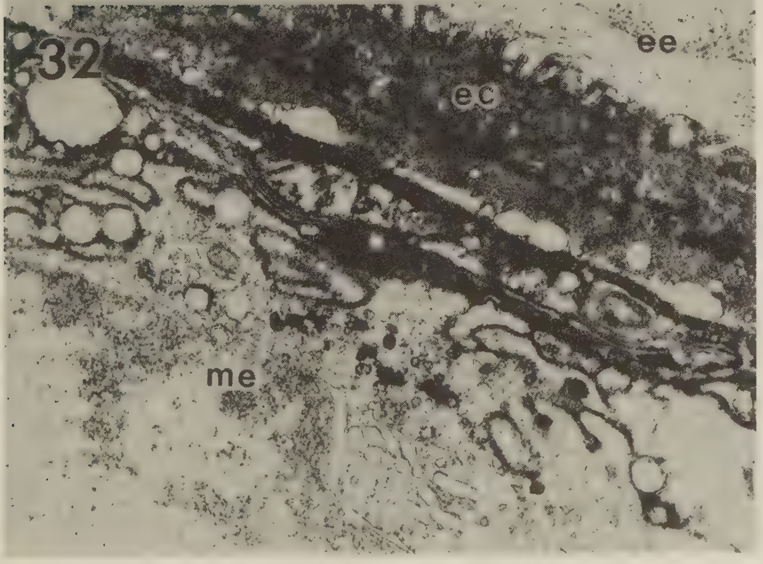


Figure 31.
The placenta of *M. griseus* administered HRP for 40 min. The reaction product appears in the narrow space between embryonic epithelium (ee) and egg capsule (ec). × 150.

me: maternal epithelium.

Figure 32.
Electronmicrograph of the placenta of *M. griseus* administered HRP for 40 min. The reaction products are detected in the apical portion of maternal epithelial cell (me) and egg capsule (ec). × 19,100.

Table 3.
Trophic relationships in developing embryos.

Reproductive mode	Species	Egg diameter (mm)	Embryo weight (g)	$\frac{\text{Embryo weight}}{(\text{Egg diameter})^3} \times 10^3$
Type I. Uterus-Oophagous	*Alopias pelagicus*	10	250	250
	Lamna ditropis	3	3710	137000
Type II. Uterus-Yolk Sac	*Orectolobus japonicus*	40	120	1.8
	Squatina japonica	40	80	1.3
Type III. Uterus-Yolk Sac	*Triakis scyllia*	20	50	6.3
	Mustelus manazo	15	57	17.0
Type IV. Uterus-Placental	*Mustelus griseus*	15	73	21.6
	Prionace glauca	8	200	391
	Scoliodon laticaudus	1	9	9000

not be detected in the embryonic epithelial cells and in capillaries under the epithelium (Fig. 32). This suggests that epithelial cells of embryonic placenta cannot take up macromolecular-weight organic materials of at least 40000 MW (MW of HRP) and that placental transport of macromolecular weight materials are minimal in *M. griseus*. These results of tracer experiments suggest that the placenta of *M. griseus* is primitive in embryonic nutrition transport.

IV. Trophic Relationship Between Mother and Embryo

Nutritive dependency indices (NDI), which were estimated from the maximum diameters of ovarian ova and embryo weight, are shown in Table 3. The values for *L. ditropis* and *A. pelagicus* were very high (1.37×10^5 in *L. ditropis* and 250 in *A. pelagicus*), although they were underestimated because the embryos of both these species were mid-term. In the placental groups the values are distributed in a wide range from 21.6 (*M. griseus*) to 9000 (*S. laticaudus*). The NDI of *M. griseus* was near those of *T. scyllia* (6.3) and *M. manazo* (17.0) which are included in the type III uterus-yolk sac. This may suggest that *Mustelus* is in a transitional state of placental differentiation. Table 3 must be considered preliminary until more information is available to increase its accuracy and usefulness.

Discussion

In chondrichthyan fishes, oviparity is considered to be a primitive, less specialized mode of reproduction (Wourms et al. 1988). Oviparity involves the deposition of ova, enclosed in a capsule, outside the maternal body. In contrast, viviparity involves the retention of internally fertilized ova in the uterus where embryonic development is completed (Wourms et al. 1988). Since all oviparous chondrichthyan fishes employ internal fertilization, the transition from oviparity to viviparity was probably uncomplicated. There are several oviparous species whose mode of reproduction may represent a transitional phase from oviparity to viviparity. *Galeus* and *Halaelurus* are examples as they show 1) the retention of the developing egg in the oviduct for long periods; 2) a tendency toward multiple oviparity; 3) a reduction in the thickness of the egg case; and 4) a loss of the surface ornamentation used for egg case attachment (Wourms et al. 1988). Since all oviparous species, including the transitional species, possess a noncompartmentalized oviduct (uterus), early viviparous species would not have uterine compartments.

In species with type II uterus, embryonic nutrients, except for the yolk reserve, are supplied through uterine secretion. The intrauterine mucosal specialization for secretion could have aided in the divergence of viviparity. Rays, *Gymunura micrura* (Wourms and Bodine 1983, 1984) and *Rhinoptera bonasus* (Hamlett et al. 1985) develop highly secretive intrauterine mucosal processes called trophonemata and are capable of an extreme matrotrophic state. They are categorized as the placental analogues mode by Wourms (1977). I suspect that this type is a final phase of the type II uterus, although it does not occur in sharks.

The type I uterus (oophagous species) occurs in five families of the order Lamniformes: Odontaspidae, Pseudocarchariidae, Alopiidae, Cetorhinidae, and Lamnidae. Lamnids include the genera, *Eugomphodus*, *Odontaspis*, *Pseudocarcharius*, *Alopias*, *Cetorhinus*, *Isurus*, *Lamna*, and *Carcharodon* (Wourms et al. 1988). In these sharks the embryo obtains nutrients from eggs continuously ovulated during gestation and sometimes from the ingestion of siblings (Springer 1948; Fujita 1981; Otake and Mizue 1981; Gilmore 1983; Gilmore et al. 1983). This group is quite specialized in the nutrient transport routes, including the physiological adaptations for egg production and ovulation. But since the uterus is not compartmentalized, this mode may be derived from species of the type II uterus (yolk sac).

The shark yolk-sac placenta is established by a stable connection between the embryonic yolk sac and the intrauterine epithelium of the mother (Mahadevan 1940; Senta and Sarangdhar 1948; Gilbert and Schlernitzauer 1966; Schlernitzauer and Gilbert 1966; Graham 1967; Teshima and Mizue 1972; Teshima 1975; Wourms 1977, 1981; Hamlett et al. 1985a,b,c; Otake and Mizue 1985; Wourms et al. 1988). In the process of shark placental differentiation it seems to be essential that the yolk sac maintains contact with the intrauterine mucosa over a long term. The uterine compartment serves to separate each embryo into a restricted space and allows this stable juxtaposition between the embryonic yolk sac and the intrauterine mucosa to be made. This contact would be a first step in forming a complex interdigitation between the yolk sac and the intrauterine mucosa, that is to say, yolk-sac placenta, excluding the physiological and immunological problems. The establishment of a uterine compartment may be an essential factor allowing the differentiation of placentation type in sharks.

Placental species occur in 17 genera within five closely related families: Leptochariidae, Triakidae, Hemigaleidae, Carcharhinidae, and Sphyrnidae (Wourms et al. 1988). They all establish uterine compartments, except for *Carcharhinus dussmieri*, which carries only one embryo in each uterus (Teshima and Mizue 1972). Furthermore, the genus *Mustelus* (Triakidae) contains both type III uterus (*M. manazo*) and type IV uterus (*M. griseus*). This suggests that these two reproductive modes are closely related to each other. The placental sharks may have evolved from species having uterine compartments. Therefore it is reasonable to divide shark viviparity into two groups by the presence or absence of uterine compartments (Table 2).

The evolution of viviparity is associated with the increase of embryonic nutrient dependency on a matrotroph (Wourms 1977, 1981; Wourms et al. 1988). Except in oophagous species, intrauterine and placental epithelia are the most important sites for the matrotrophic nutrient transport route. The nutrient transport function of these

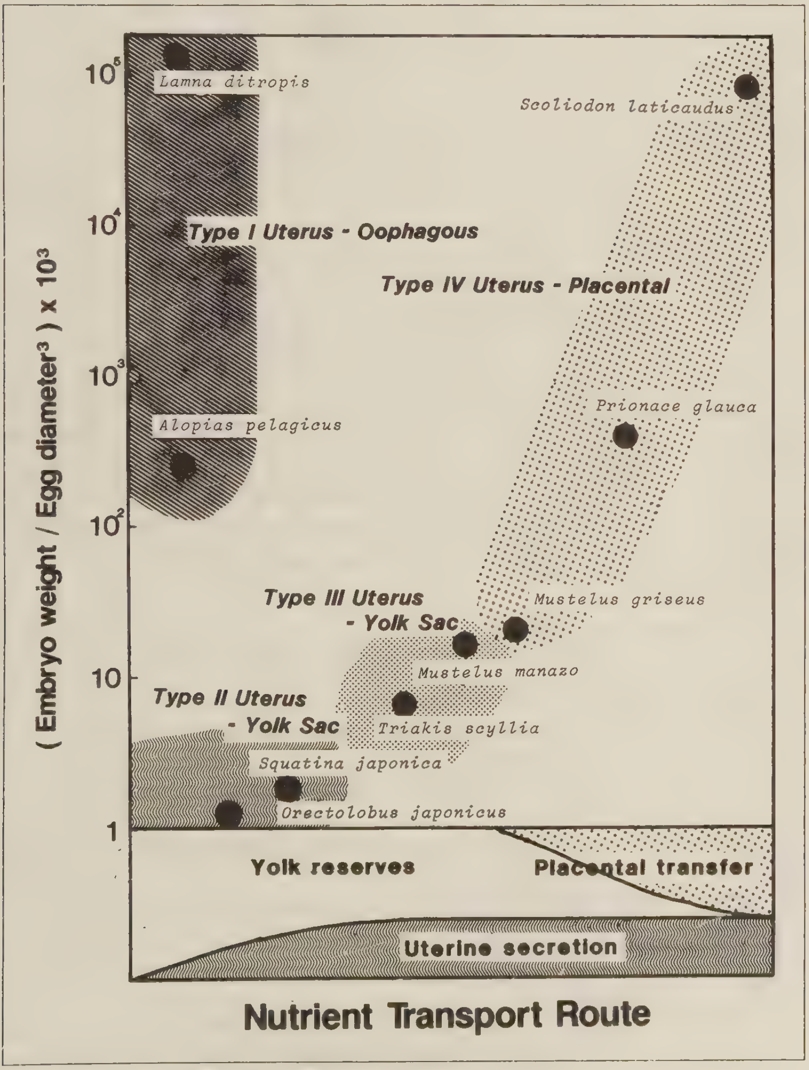


Figure 33.
Trophic relationships between mother and embryo and the embryonic nutrient transport route.

tissues directly represents the nutritive relationship between mother and embryo. Therefore, the evolutionary level of each reproductive mode should be revealed by the histological features of the intrauterine and placental epithelia. In species with a type II uterus, the secretive activity increases in the following order: *O. japonicus*, *S. japonica*, and *S. mitsukurii*. The intrauterine epithelia of species of the two type III uterus, *T. scyllia* and *M. manazo*, are significantly more active in secretion than those of type II uterus species. Within this former group my histological examinations show that *M. manazo* probably depends on parental embryonic nutrient sources more than *T. scyllia*. In placental species, the state of placental differentiation would be indicated by morphological adaptations, which facilitate the transport of nutrients and waste products. An egg capsule which intervenes between the maternal and embryonic epithelia is certainly a barrier to macromolecular nutrient transport as demonstrated in my tracer experiments using HRP and trypan blue, although water and low molecular weight materials such as glucose pass through the membrane (Graham 1967). The placenta of *M. griseus*, which retains the egg capsule through gestation, probably represent the primitive condition. In contrast, *Scoliodon* loses the egg capsule and establishes a haemotrophical nutrition transport system but these are relatively advanced characteristics. Evolutionarily, *Prionace* is in an intermediate position. The egg capsule degenerates in the placenta during gestation. Uterine secretion seems to have a role in embryonic nutrition in both *M. griseus* and *S. laticaudus*. In these species both placental and uterine secretion are present. The relative importance of placental transport and uterine secretion is unknown and should be a topic of future research.

The increase of embryonic organic material during gestation indicates the nutrient dependency of the embryo on matrotroph as demonstrated by Ranzi (1932, 1934); Amoroso (1960); Stribling et al. (1980); Wourms (1977, 1981); and Wourms et al. (1988). The nutritive dependency, a result of the trophic relationship between mother and embryo, seems to be one of the important indices that could be used to represent the evolutionary state of viviparity. In the present study, NDI values of viviparous sharks in each reproductive mode are grouped and increase in the following order: type II uterus–yolk sac; type III uterus–yolk sac; type IV uterus–placental; and type I uterus–Oophagous species. Figure 33 shows the relationship between the NDI values and the nutrient transport route estimated from histology of the intrauterine epithelium and placenta. Species in the lower and left portion of the figure may be considered primitive in the development of viviparity. More advanced species appear in the upper and right portion, except the oophagous species whose embryos are characteristically nourished by the yolk of ovulated eggs. Based on my results, the evolutionary development of viviparity in sharks might follow the pattern shown in Fig. 34.

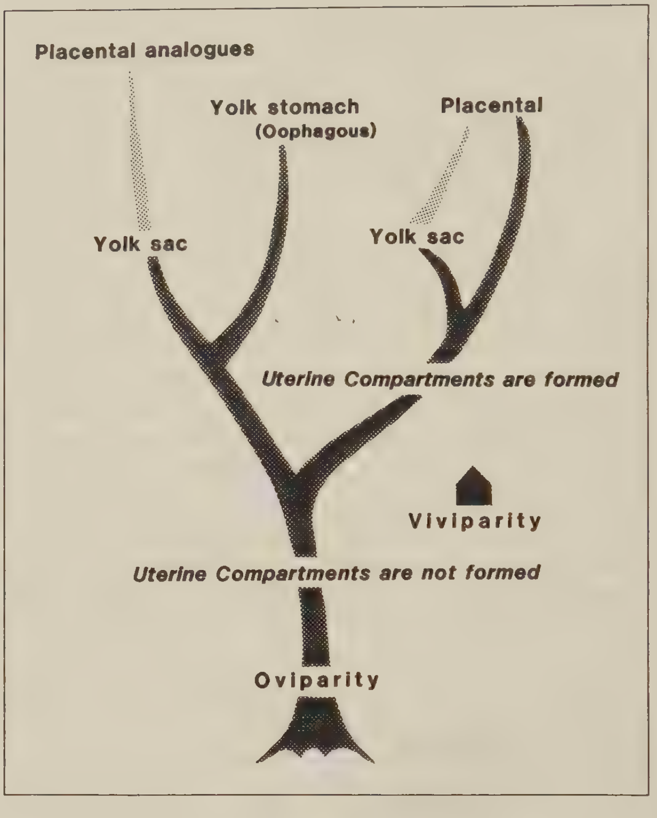


Figure 34.
Evolutionary development of viviparity in sharks.

Acknowledgments

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An Overview of Chondrichthyan Seminiferous Follicles Using Electron Microscopy

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ABSTRACT

Later stages of spermatogenesis and mature spermatozoa of seven species of chondrichthyan fishes were examined using electron microscopy and compared with regard to their systematic position. Four species of sharks: *Prionace glauca*, *Carcharhinus falciformis*, *Centroscymnus owstoni*, and *Chlamydoselachus anguineus*; two species of rays: *Dasyatis kuhlii* and *Dasyatis garouaensis*; and one species of chimaera: *Chimaera phantasma* were examined in this study. Seminiferous follicles of these fishes contained many sperm clumps which were composed of about 64 spermatozoa. The sperm clumps of the four sharks were arranged regularly with the heads of the spermatozoa turned toward the basement membrane of the follicle. The sperm clumps in *C. anguinesus* were loosely arranged compared with those of the other three sharks. In rays, the clumps were not regularly arranged in the follicle (and were dissolved in the final stage of spermatogenesis). The follicle and sperm clump of *C. phantasma* were morphologically similar to those of sharks. Among the three taxonomic groups, the longitudinal column (LC) of the tail of mature spermatozoa was different in shape and number of columns. The spermatozoa of sharks had two LC which were located on both sides of tail flagellum and oval shaped with flattened interior surfaces when viewed in cross section. Spermatozoa of rays also had two LC which were round in cross section. In *C. phantasma*, only one round LC was present.

Introduction

Previous light microscopy observations on the spermatogenesis of elasmobranchs (Chen et al. 1973; Matthews 1950; Stanley 1966) revealed few differences among elasmobranchs and between elasmobranchs and chimaeras. Recently, observations of chondrichthyan tissues, using electron microscopy, have increased (Stanley 1971a,b; Hara 1978; Tanaka et al. 1978; Takemura et al. 1983) and structure of the spermatozoon and details of spermatogenesis have been elucidated. However, the fine structure of the entire seminiferous follicle in the testis has not been investigated using electron microscopy. For this overview, fresh specimens of the testes of sharks, rays, and chimaeras were observed using both scanning electron microscopy (SEM) and transmission electron microscopy (TEM). The ultrastructure of mature spermatozoa and seminiferous follicles of these fishes are described and compared.

Materials and Methods

Four species of sharks: *Prionace glauca*, *Carcharhinus falciformis*, *Centroscymnus owstoni*, and *Chlamydoselachus anguineus*; two species of rays, *Dasyatis kuhlii* and *Dasyatis garouaensis*; and one species of chimaera, *Chimaera phantasma* were used in this study. Testes were cut into 2–3 mm cubes, which were prefixed with 0.5% paraformaldehyde and 2% glutaraldehyde in 0.1M cacodylate buffer with 7.5% sucrose overnight or as long as three weeks. Samples were rinsed overnight in the above buffer followed by a two-hour postfixation in 1% osmium tetroxide in the same buffer. For SEM investigation, testes were dehydrated in ethanol,

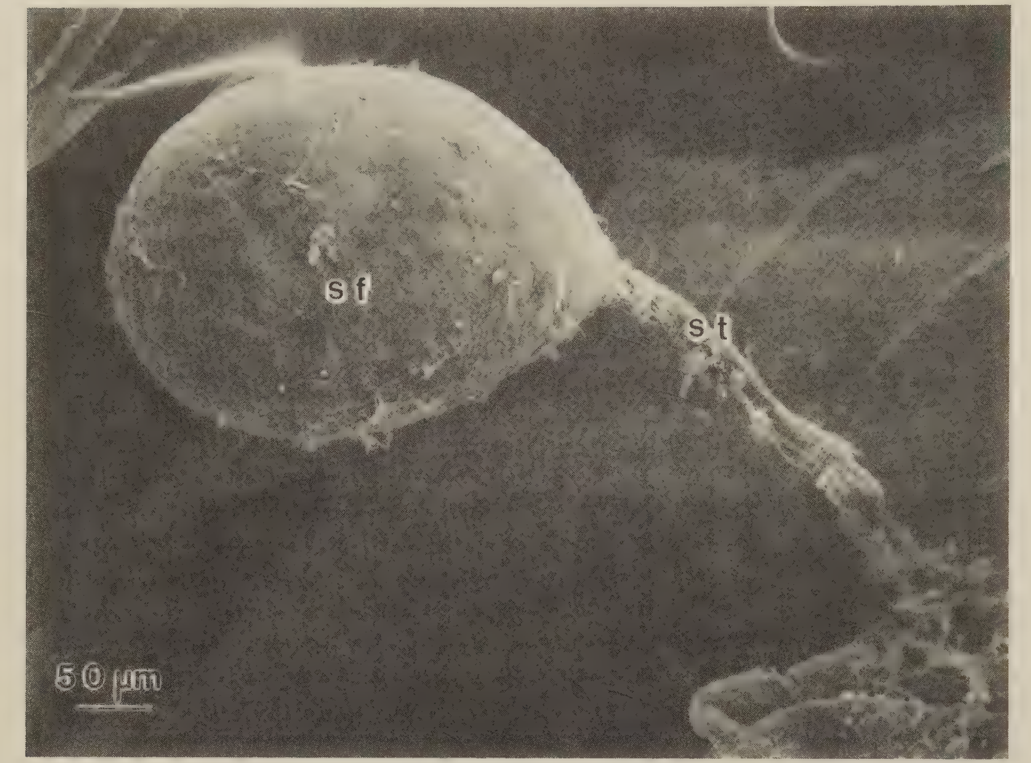

Figure 1.
Scanning electron micrograph of *Chlamydoselachus anguineus* seminiferous follicle. sf: seminiferous follicle, st: seminiferous tubule.

dried in CO_2 using the critical point method and sputter-coated with gold. For TEM, samples were dehydrated in ethanol and embedded in Epon 812 (TAAB Laboratories Equipment Limited).

Survey sections (about 1.1 × 2.0 mm) were cut and stained with toluidine blue following the method of Sakai (1982). To choose an appropriate grid size, various sizes of mesh were superimposed on the survey sections. Grids with an open area of 500 × 666 μm were selected for large sections and survey section blocks were trimmed to fit the grid area. Sections were cut to a thickness of 100 to 130 nm with a diamond knife mounted in a LKB Ultratome V. Section thickness was estimated using a scale calibrated with interferrence colors. The sections were then mounted on grids and stained in a saturated solution of uranyl acetate for 20 minutes, then in lead citrate for six minutes.

Finally, cells were observed and photographed using an AKASHI LEM-2000 wide-field electron microscope, a JEM 100 CX electron microscope, and an AKASHI DS-130 scanning electron microscope.

Observations

SEM Observations of a Chondrichthyan Seminiferous Follicle

The mature testis is composed of numerous follicles containing mature spermatozoa and spermatogenic cells in various developmental stages. Each seminiferous follicle is spherical with an uneven surface and a long fine efferent tubule (Fig. 1). Spermatozoa are thought to be transported to the epididymis through the efferent tubule when the seminiferous follicle matures.

Super Wide-Field TEM Observations of Sectioned Follicles

Mature seminiferous follicles of these seven species of chondrichthyan fishes contained many sperm clumps each with about 64 spermatozoa. Sertoli cells were arranged in the follicles' basement membrane in all shark species investigated (Figs. 2–5). The sperm clumps of the four shark species were arranged regularly with the heads of the spermatozoa turned toward the basement membrane of the follicle. The clumps of *C. anguineus* (Fig. 5) were loosely arranged compared with those of *C. owstoni*, *C. falciformis*, and *P. glauca*. In rays, the clumps appear not to be regularly arranged in the follicle (Figs. 6, 7). The clumps were broken down in the final stage of spermatogenesis (Fig. 7). The follicle and sperm clumps of *Chimaera phantasma* were morphologically similar to those of sharks (Fig. 8).

Fine Structure of Mature Spermatozoa

The spermatozoa of these chondrichthyan fishes were between 110 and 150 μm in total length. The spermatozoon is composed of a head, neck, and tail. We compared cross sections of these three parts of the spermatozoon among

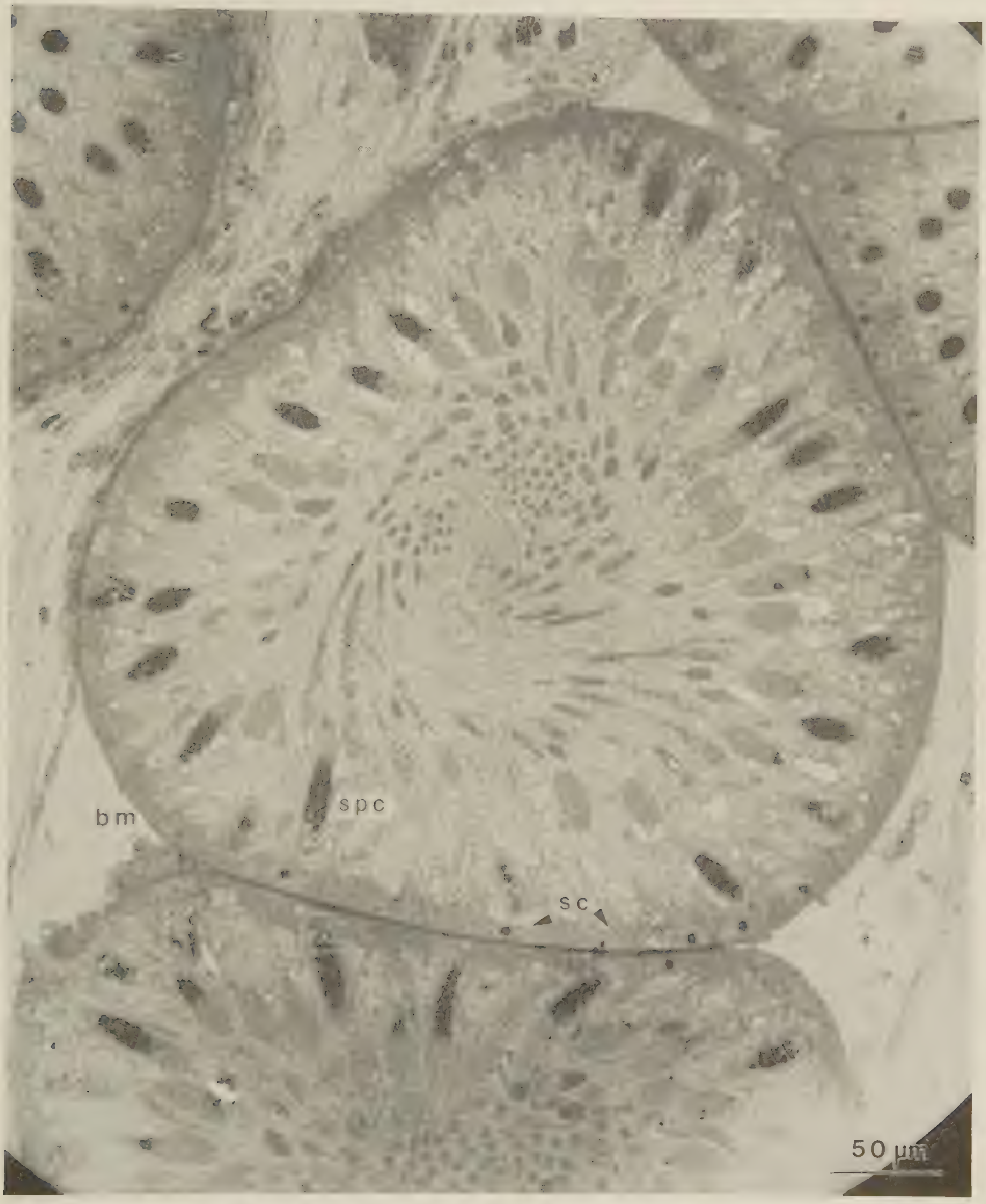

Figure 2.
Super wide-field electron micrograph of *Prionace glauca* seminiferous follicle. (Slightly off center section). bm: basement membrane, sc: sertoli cell, spc: sperm clump.

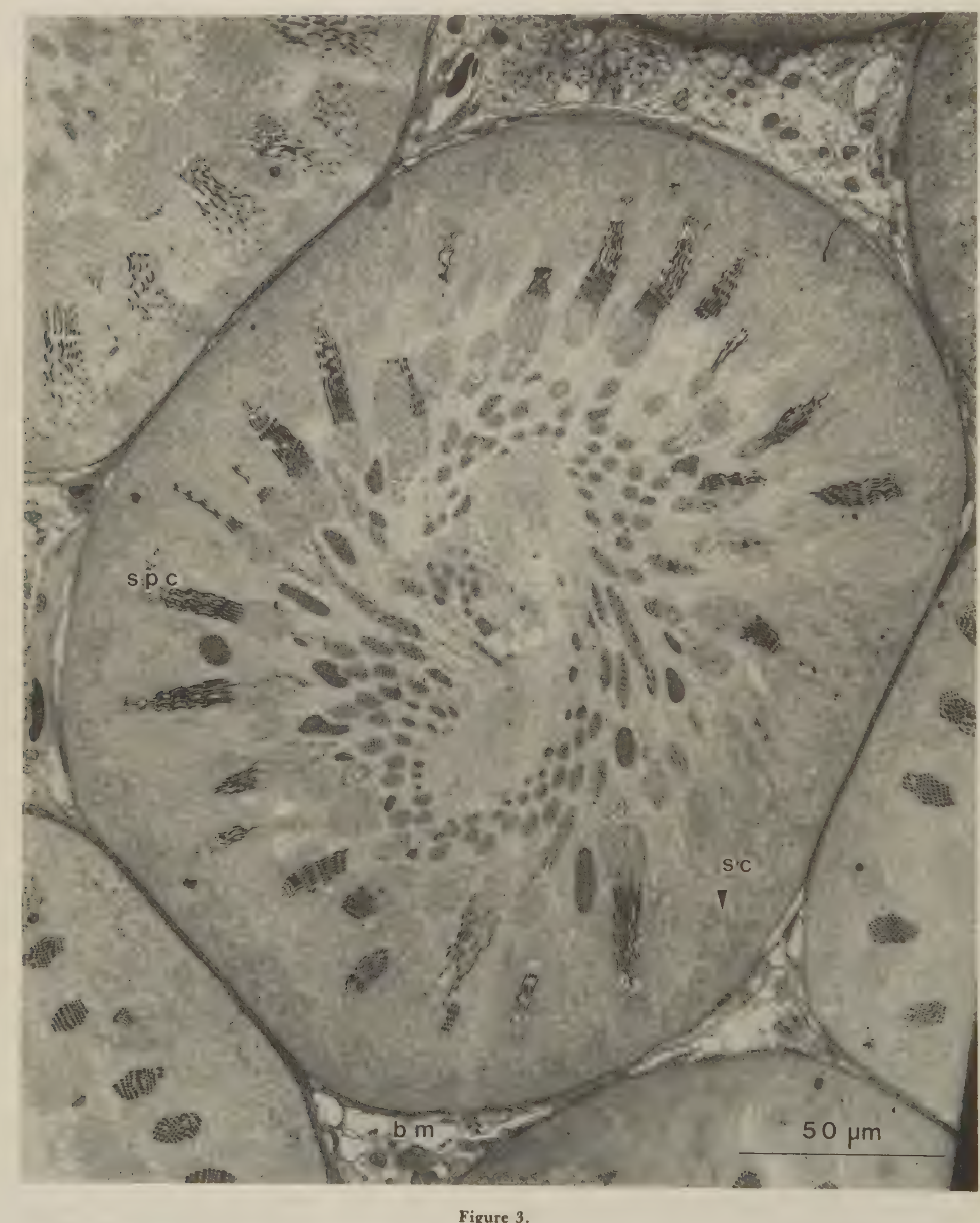

Figure 3.
Super wide-field electron micrograph of *Carcharhinus falciformis* seminiferous follicle. bm: basement membrane, sc: sertori cell, spc: sperm clump.

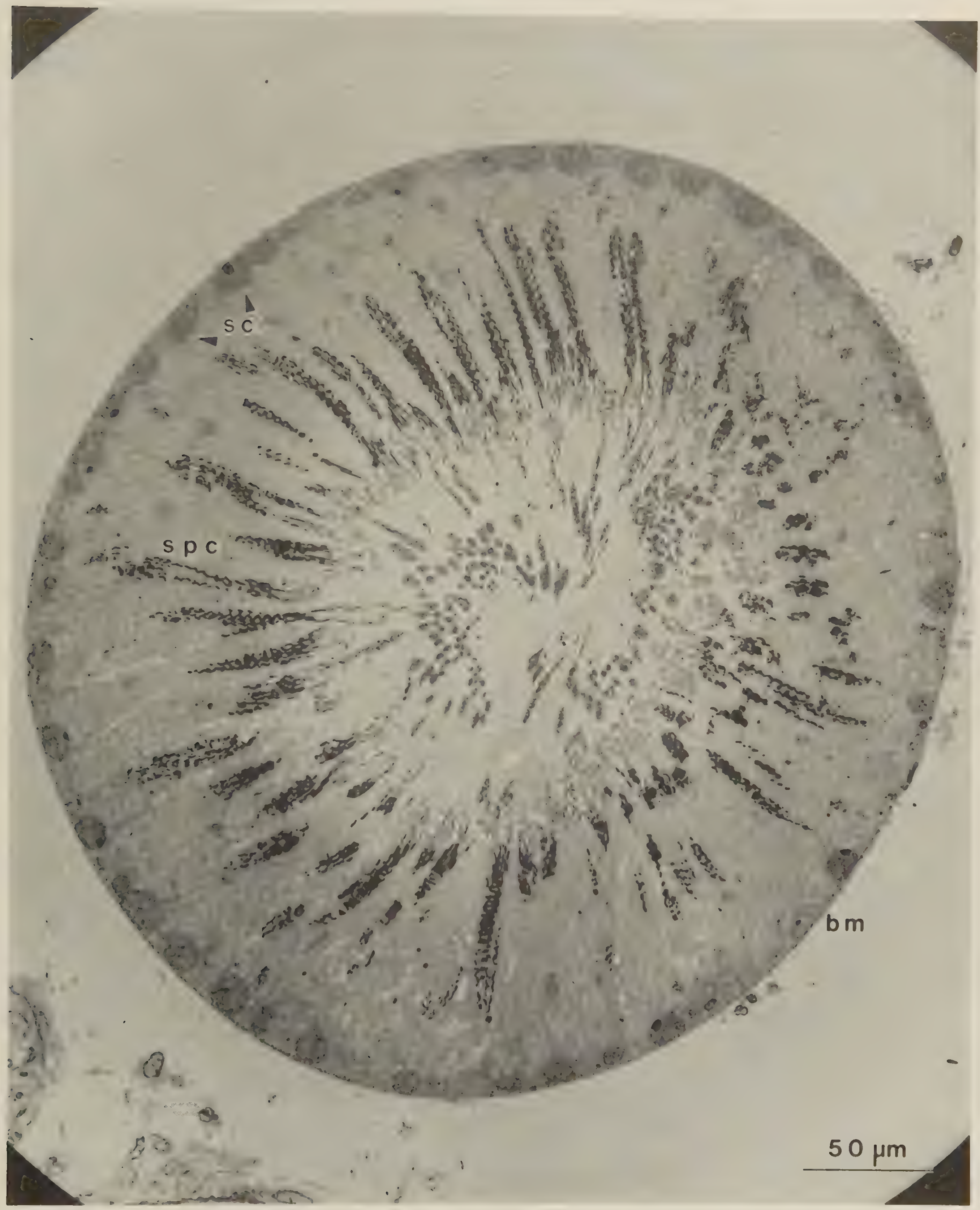

Figure 4.
Super wide-field electron micrograph of *Centroscymnus owstoni* seminiferous follicle. bm: basement membrane, sc: sertoli cell, spc: sperm clump.

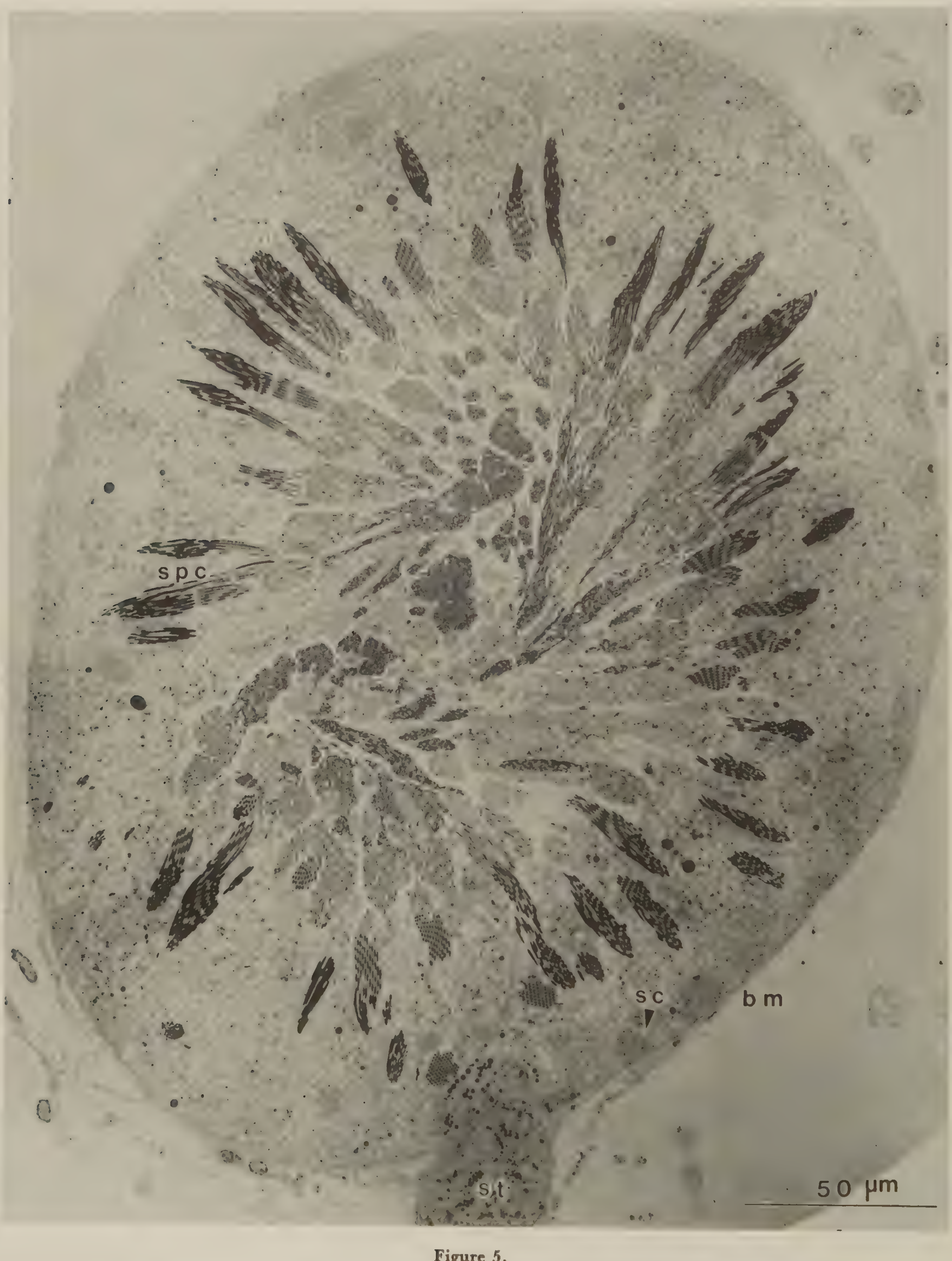

Figure 5.
Super wide-field electron micrograph of *Chlamydoselachus anguineus* seminiferous follicle. bm: basement membrane, sc: sertoli cell, spc: sperm clump, st: seminiferous tubule.

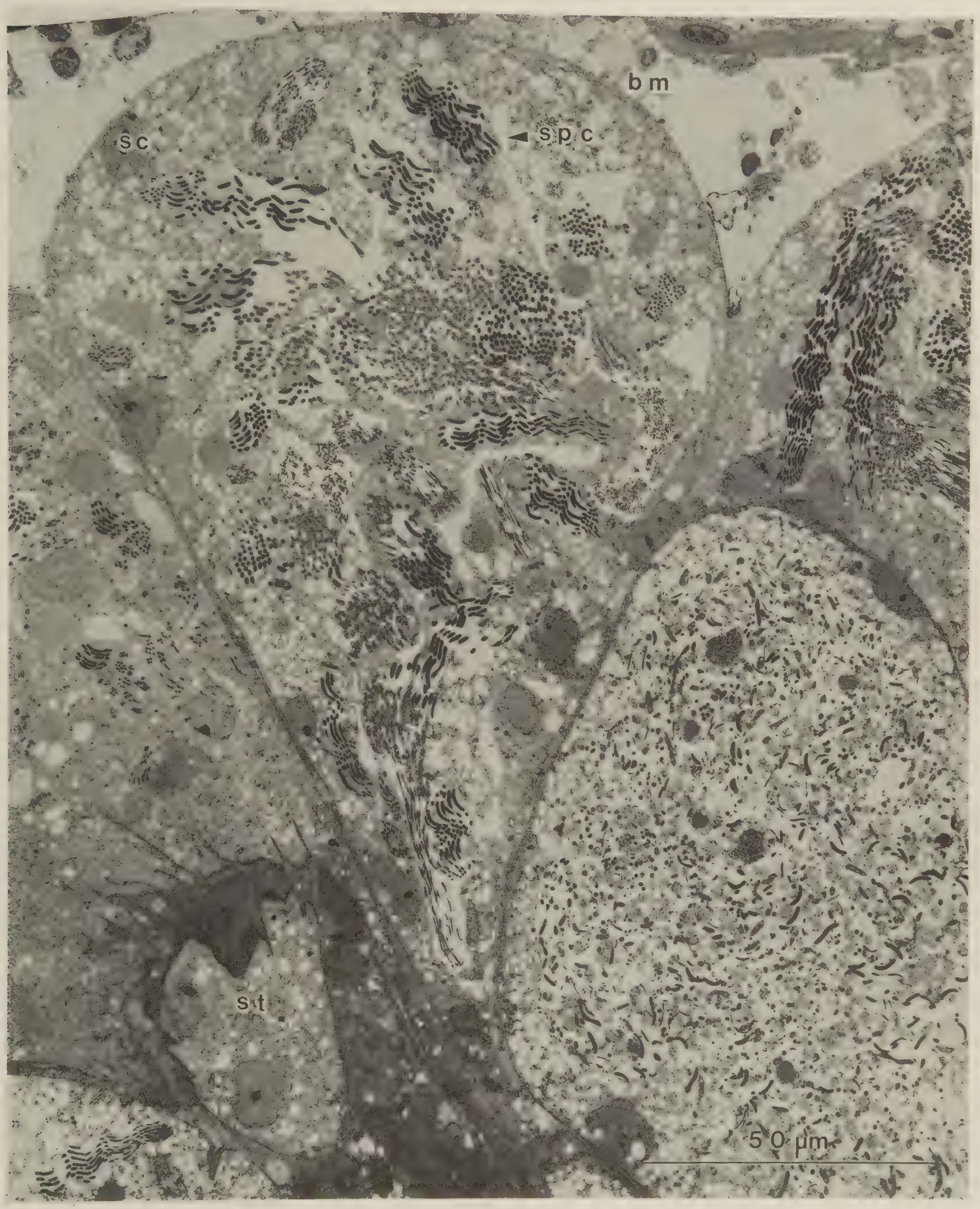

Figure 6.
Super wide-field electron micrograph of *Dasyatis kuhlii* seminiferous follicle. bm: basement membrane, sc: sertoli cell, spc: sperm clump, st: seminiferous tubule.

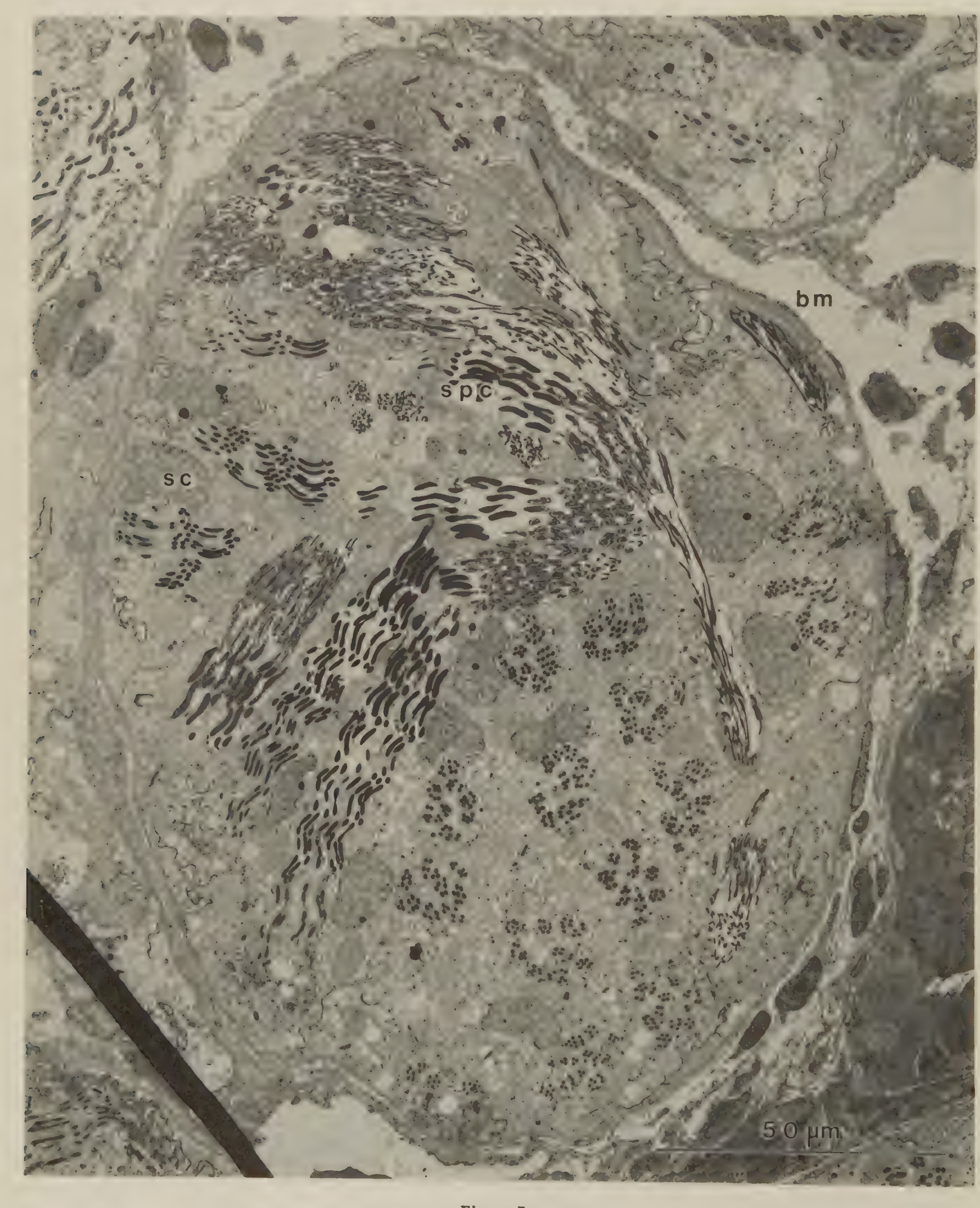

Figure 7.
Super wide-field electron micrograph of *Dasyatis garouaensis* seminiferous follicle with sperm clumps broken down. bm: basement membrane, sc: sertoli cell, spc: sperm clump.

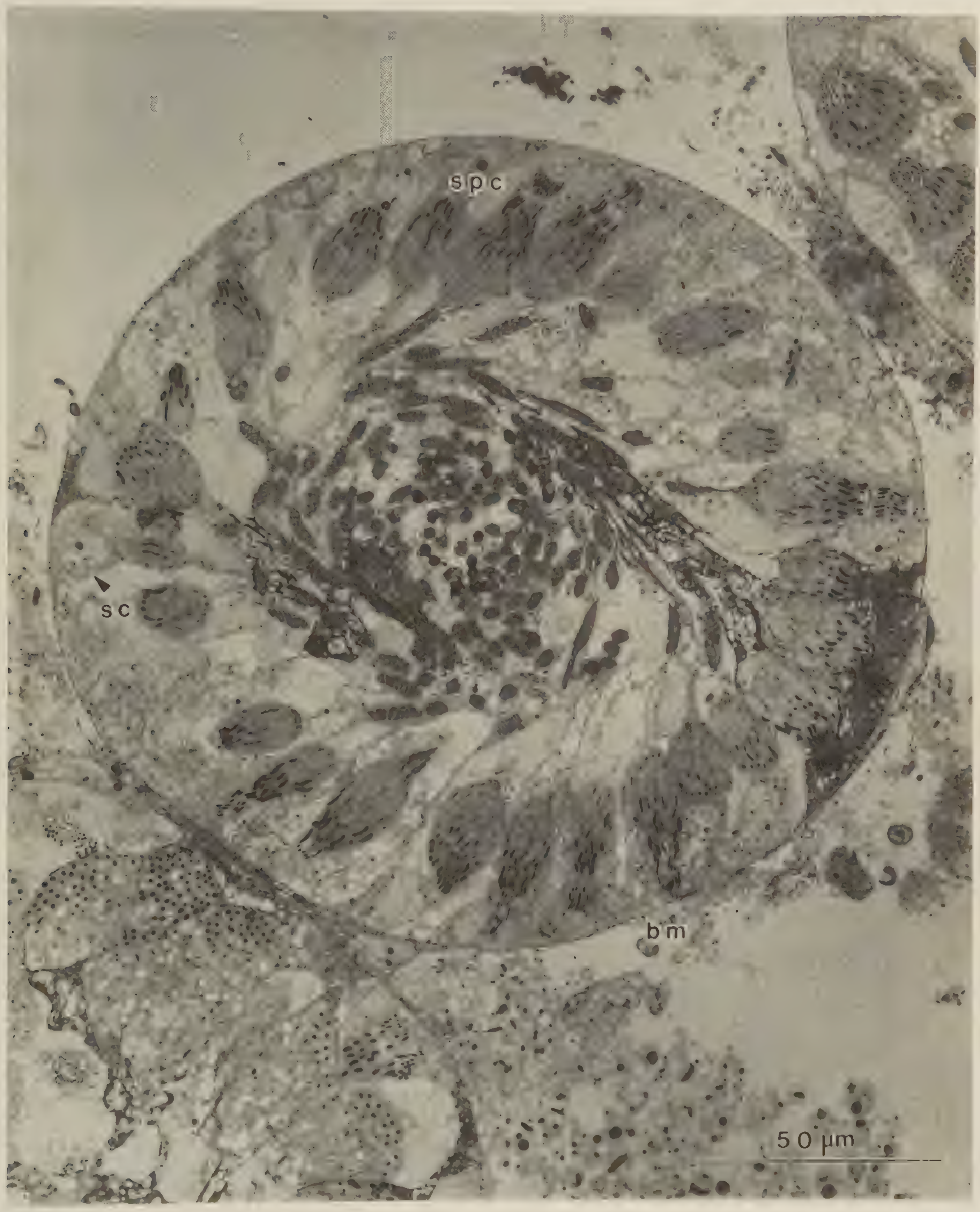

Figure 8.
Super wide-field electron micrograph of *Chimaera phantasma* seminiferous follicle (not fully matured). bm: basement membrane, sc: sertoli cell, spc: sperm clump

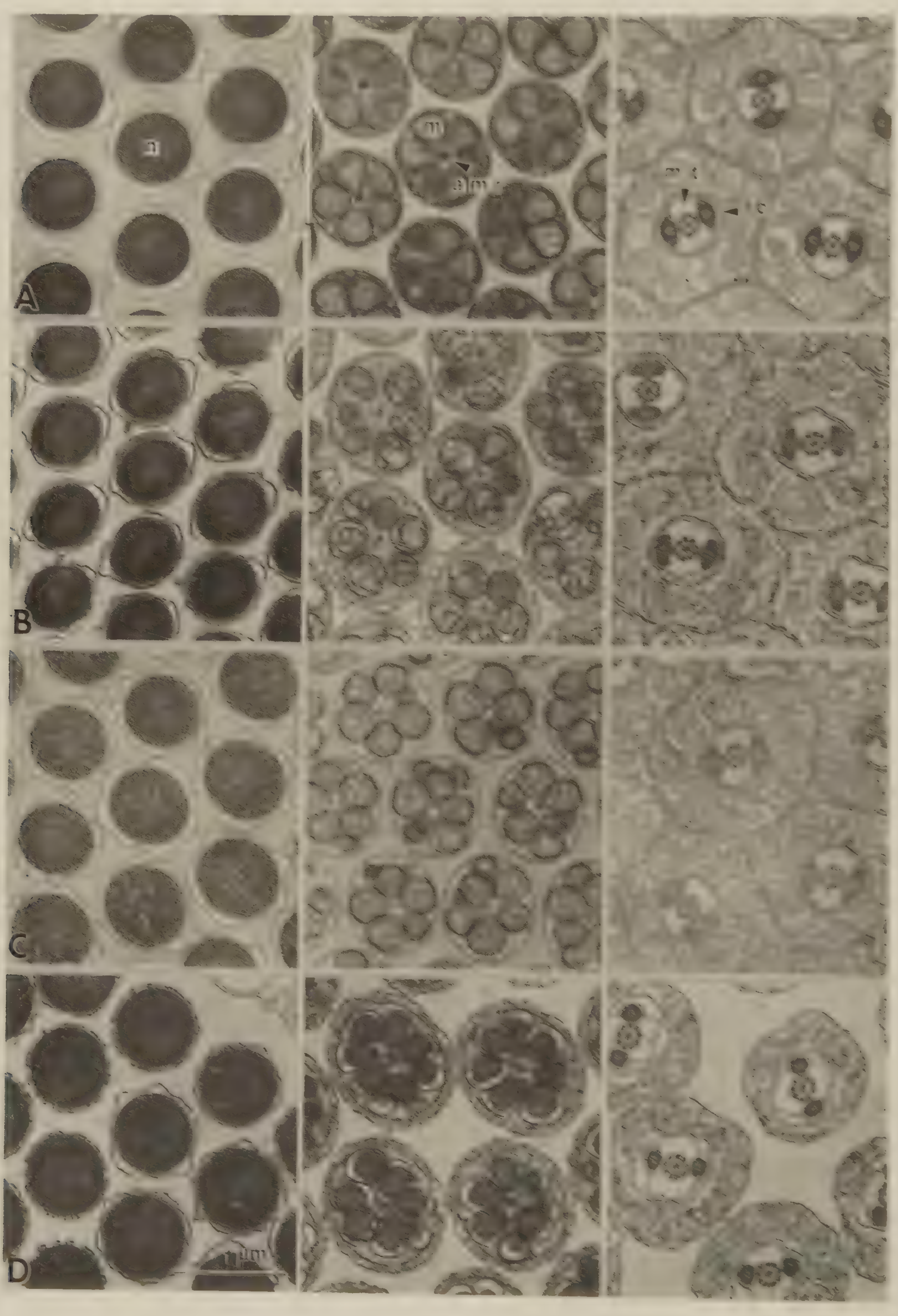

Figure 9.

Cross sections of head, neck and tail of spermatozoa taken from mature seminiferous follicles. A. *Prionace glauca* B. *Carcharhinus falciformis* C. *Centroscymnus owstoni* D. *Chlamydoselachus anguineus*. n: nucleus, amr: axial midpiece rod, mt: microtubule, lc: longitudinal columns

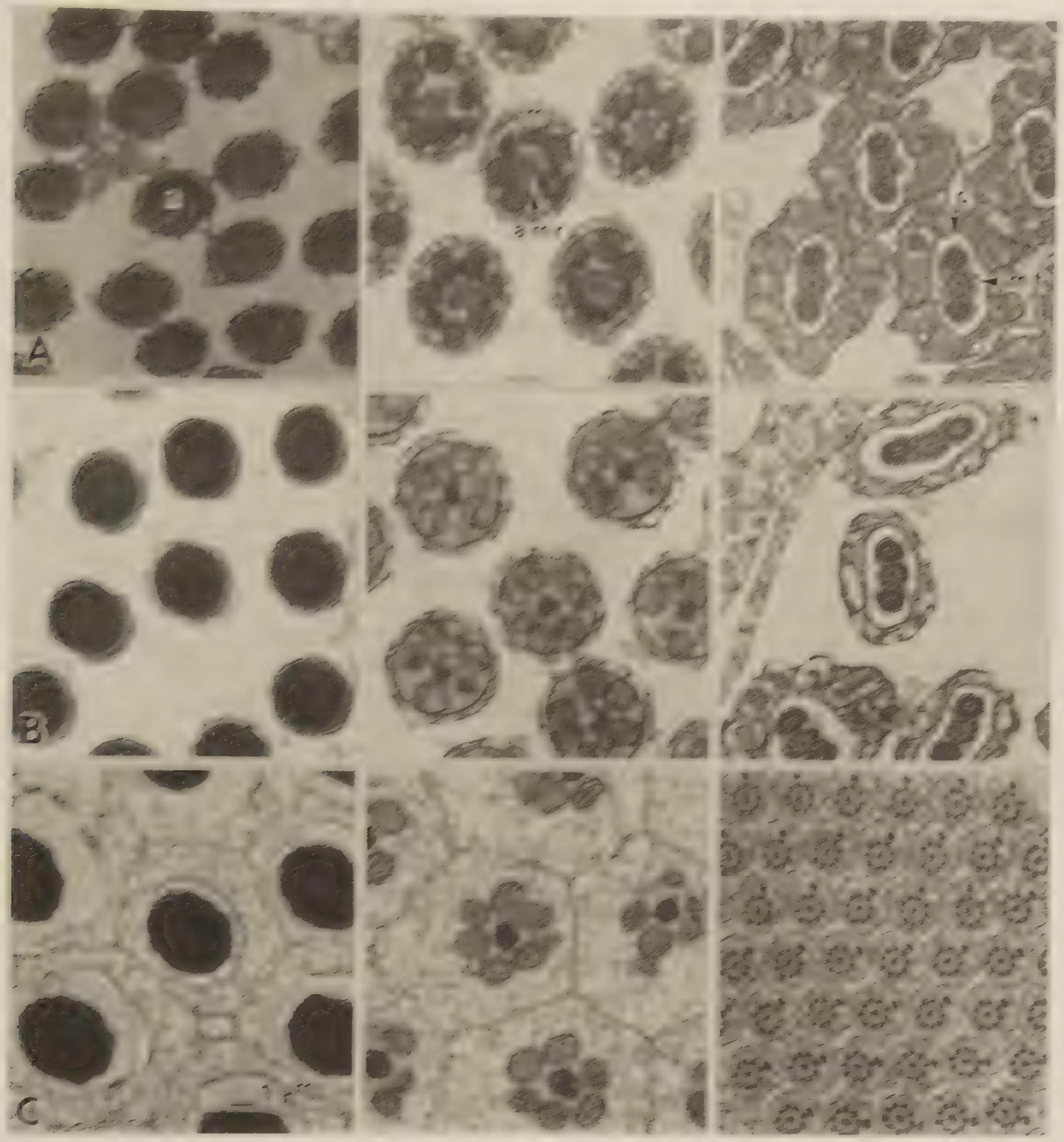

Figure 10.

Cross sections of head, neck and tail of spermatozoa taken from mature seminiferous follicles. A. *Dasyatis akajei* B. *Dasyatis* [illegible] C. *Chimaera phantasma*. n: nucleus, amr: axial midpiece rod, mt: microtubule, lc: longitudinal column.

the seven species. The head, comprised of compressed nuclear granules, is of high electron density (Figs. 9, 10). The neck consists of the midpiece rod surrounded by five to six mitochondoria. The midpiece rod of the sharks examined is much more slender than that of the rays and that of chimaera which we investigated (Figs. 9, 10). The spermatozoan tail consists of a tail flagellum and a longitudinal column (LC). The tail flagellum has a pair of microtubules in the center and nine pairs around the center. In the sharks, two LC's (oval in cross section), are seen on both sides of the tail flagellum. The structure of the LC is tubular with a microfiber in the center. Rays also have two LC's, but their shapes were rounded rather than oval. In chimaera, only one rounded LC was present.

Conclusion

Although our study covers only a few chondrichthyan species, electron microscopy reveals mosaic patterns (Figs.

9, 10) which may be associated with the systematic relationships of sharks, rays, and chimaeras. The loose arrangements of sperm clumps seen in *Chlamydoselachus anguineus* follicles may also have systematic value when compared to other sharks. Differences in function may also account for the morphological variation seen in these species.

In the future, we hope to investigate and compare these features among elasmobranchs in the hope of contributing to the clarification of the systematics of these interesting animals.

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Serum Levels of Circulating Steroid Hormones In Free-ranging Carcharhinoid Sharks

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ABSTRACT

Requiem sharks of the family Carcharhinidae and the closely related sphyrnid or hammerhead sharks are the only lower vertebrates to possess placental viviparity. In contrast to the well-known role of steroid hormones in regulating reproductive processes in mammals, little information exists on the type, amount, seasonal timing, or reproductive variations of steroid hormones in these two shark families. In this study baseline values were measured for four circulating steroid hormones: estradiol, progesterone, testosterone and dihydrotestosterone. Additionally, corticosterone and progesterone, often associated with stress responses, were measured in eleven species of sharks. Of special interest were the elevated serum estradiol and testosterone levels from actively courting female lemon sharks and from female blacknose and hammerhead sharks with large ova in the ovary.

Introduction

The largest family of sharks, the Carcharhinidae or requiem sharks, as well as the sphyrnid sharks, contains species with placental viviparity, a unique biological feature for reproduction in lower vertebrates (Springer 1960; Wourms 1977; Gilbert 1981; Teshima 1981; Parsons 1983; Campagno 1984). By definition viviparous species of these two families, including the focal species of this report, the lemon shark *Negaprion brevirostris*, give birth to living young (Gruber 1982, 1988). Young are carried to full-term within the uterus of the female, with access to the maternal blood supply by an umbilical attachment to a placenta (Wourms 1981, 1987; Hamlett 1987; Wourms et al. 1988). The placenta, formed from the yolk sac, a structure analogous to the chorion-amnionic membrane of mammals, connects with the epithelium of the maternal uterus (Jollie and Jollie 1967; Hamlett et al. 1985a,b,c). The degree of interattachment and interdigitation of the maternal and fetal tissues differs considerably between species (Jollie and Jollie 1967; Hamlett 1987; Otake and Mizue 1986). Wourms (1977) noted that in some cases "based on embryological origin and adult morphology, their . . . reproductive system is more similar to tetrapods than teleosts."

Steroid hormones, such as 17-β estradiol (E_2), progesterone (P), testosterone (T) and dihydrotestosterone (DHT), usually associated with mammalian reproduction have not been to our knowledge investigated in the carcharhinoids. In contrast, substantial information exists describing the biochemistry and circulating patterns of some of these hormones in aplacental sharks, such as the ovoviviparous spiny dogfish *Squalus acanthias*, and the oviparous catsharks, including *Scyliorhinus caniculus*, as well as several batoids and rajoids. For these elasmobranchs, tissue sources of reproductive hormones such as estrone (E_1) and 17-β estradiol (E_2) (Gottfried 1964; Simpson et al. 1964; Callard and Leathem 1965; Craik 1979), E_1, E_2, and progesterone (P) (Hisaw 1959; Dodd et al. 1960; Wotiz et al. 1960; Liley 1969; 1960; Klosterman and Callard 1986; Koob et al. 1986; Tsang and Callard 1983), testosterone (T) (Chieffi 1967; Dobson and Dodd 1977;

Callard et al. 1985) and their circulating blood levels (Sumpter and Dodd 1979; Dodd 1983; Darrow and Fletcher 1972: Tsang and Callard 1987, 1988) have been reported. The influence of the pituitary on hormone levels and reproductive processes has been investigated by Hoar (1965), Dodd (1972, 1983), and Dobson and Dodd (1977).

The primary objective of this study was to establish normal concentrations and ranges of selected steroid hormones in the serum of carcharhinoid sharks. In the present study, serum samples were obtained from ten species of viviparous and one species of ovoviviparous sharks. These included mature and immature specimens of both sexes in various stages of their reproductive cycles.

We also measured corticosterone in the 11 species. The only other comparable study in the carcharhinoids is that of Honn and Chavin (1978). They determined levels of adrenocorticotrophic hormone (ACTH) in the blue shark *Prionace glauca*.

The influence of the pituitary has been studied in a number of nonplacental elasmobranchs including *Dasyatis sabina* (Klesch and Sage 1973). Since the stress-related corticosteroids, as well as testosterone and progesterone, are known to affect behavior in a number of higher vertebrates (Fraile et al. 1987), we concentrated on elasmobranch analogues because of the possibility that they might also affect behavior. We thus measured corticosterone not only to establish baseline levels and ranges but to compare levels of corticoids and the putative gonadal hormones to provide evidence for their possible role in maturation and reproduction.

In this study we will show for the first time that the serum of placental sharks contains measureable levels of 17-β estradiol, testosterone, dihydrotestosterone, and progesterone. The moderate concentrations of these hormones in immature sharks suggest that they play a role in reproductive development. The high levels of 17-β estradiol and testosterone in mature female sharks further suggest a role for these hormones in reproductive cycles.

Methods

A. Shark Species

Serum samples were obtained from the following carcharhinid species: the blacknose shark, *Carcharhinus acronotus*; the bull shark, *C. leucas*; the blacktip shark, *C. limbatus*; the Caribbean reef shark, *C. perezi*; the sandbar shark, *C. plumbeus*; the tiger shark, *Galeocerdo cuvier*; the lemon shark, *Negaprion brevirostris*; and the sharpnose shark, *Rhizoprionodon porosus*. We also obtained samples from the great hammerhead, *Sphyrna mokarran*, and scalloped hammerhead, *Sphyrna lewini*, as well as from the nurse shark, *Ginglymostoma cirratum*, an orectolobid.

B. Sample Collection

1. Pilot Study—We first conducted a pilot study to determine if our standard purification and radioimmunoassay procedures for assaying mammalian steroid hormones (Resko et al. 1975, 1980) could be used with the serum of carcharhinid sharks. In 1986 we collected eight serum samples from immature captive lemon sharks (Gruber 1980; Gruber and Keyes 1981).

2. Longline Samples—Most of the field collections were obtained from specimens captured on longline fishing gear and other gear as described in Gruber (1982). The collection sites included Bonefish Hole and the flats 5-km east of Alicetown, Bimini, Bahamas. Collections were made during 2-week research cruises in May and September 1987. Time on the longline prior to sample collection ranged from less than one hour to up to four hours. Live sharks were placed in tonic immobility to facilitate venipuncture (Gruber and Keyes 1981; Zlotkin and Gruber 1984; Whitman et al. 1986).

3. Tournament Samples—Serum samples were collected from 6 species (total of 12 samples) during a sportfishing tournament in April 1987. Only mature specimens were captured and the majority of these were taken in the ocean east of Miami Beach, Florida. A few sharks were captured off the Florida Keys. The serum samples were taken from sharks that had died 1-2 hours earlier.

4. Chronic Study—We obtained serum from two reproductively active female lemon sharks caught on the longline off Bimini. The first female was tagged and released after venipuncture. The second female was transferred to a 5 × 20 m holding pen on the flats and allowed to swim freely therein. This female (241 cm precaudal length) had fresh mating scars indicating that she had recently been involved in courtship. During a five-day period of captivity, daily blood samples were removed from her caudal vein at 24-hour intervals between 1100 and 1500 hours. To collect a sample by venipuncture, we restrained the shark by hand by placing ropes around her fins, inverted her, and placed her in tonic immobility.

For comparative purposes, we maintained a mature, male nurse shark in a 1 × 2 × 5 m open seawater aquarium aboard ship. We obtained blood samples in a similar way at 0900 and 2200 hours for six days.

C. Treatment of the Blood Samples

Five to 20 mL blood samples from live sharks were collected by caudal venipuncture (Stoskopf et al. 1984). Samples were immediately placed on ice for 2-3 hours (Spurling 1981), then centrifuged for 15 minutes at 3,200 rpm (1286 × g). The resultant serum sample was frozen and stored at − 20 to − 30°C until thawed for analyses.

Samples from dead sharks were taken within two hours of death and included specimens from the shark tournaments and the research cruises.

D. Radioimmunoassay (RIA)

Serum aliquots (500 μL) were extracted with redistilled diethylether and the extract sequentially chromatographed on two separate Sephadex LH-20 chromatographic columns prior to analyses by radioimmunoassay (RIA) (Resko et al. 1975, 1980). The first column (1.0 g LH-20, elution phase, hexane:benzene:methanol (62:20:13 v/v)) separated neutral and phenolic steroids and permitted the isolation of E_1 and E_2. The second column (2.5 g LH-20, elution phase, hexane:benzene:methanol (85:15:5 v/v)) isolated P, DHT, and T.

Extraction and chromatographic losses were monitored by adding known amounts of tritiated, authentic steroids to the shark serum and by processing in parallel with the samples for assay. Respective recoveries following the final chromatographic step were E_1–80.5%; E_2–82.9%; P–79.8%; DHT–72.0%; T–70.0%. Water blanks were also processed in parallel to provide solvent and method blanks for each steroid; the blanks were low, not exceeding 15 pg in any assay. The final reported values as expressed either as pg/mL of serum or ng/mL of serum were corrected for both procedural losses and method blanks before adjustment of the aliquot sample size to equate to 1 mL serum. Each sample was diluted with 500 μL of ethanol after chromatography and assayed at three or four different volumes (between 5 and 400 μL). The reported values are the average concentration calculated from aliquots whose values fell between the 5–95% binding limits of the standard curve following a logit-log transformation (Resko et al. 1975).

Antisera (A/S) used in these RIAs were obtained either from G. D. Niswender, Colorado State University (E_2–GDN 244); or Holly Hills Biologicals, Hillsboro, OR (T/DHT-lot A-1); or Radioassay Systems Laboratory (RSL), Carson, CA (E_1–351-7; CS-SR3-38); or A. Surve, Sandoz Pharmaceuticals (P-lot #12). There was less than 0.1% cross reactivity between the antisera and only the T/DHT antisera demonstrated slightly higher cross-reactivity. Specificity was further checked by determining the degree of parallelism exhibited by the authentic steroids and varying aliquots (from 10 to 400 μL) from the appropriate corresponding chromatographic fractions collected from the original extracts of shark serum. The steroids—E_2, P, T, and DHT—isolated from shark serum demonstrated complete parallelism with the standards in the RIA, indicating the absence of substantial quantities of interfering substances. E_1 and cortisol data demonstrated nonparallel activity; in addition, the limited amount of immunoreactivity present prevented adequate documentation. Analyses of serum extract for cortisol with an A/S with limited cross reactivity for corticosterone showed minimal displacement at serum volumes up to 50 μL. Therefore, data for E_1 and cortisol are not reported.

Substantial nonparallelism was observed in the estimation of corticosteroid concentrations after diethylether extraction without further purification, using RSL corticosterone A/S. While not directly tested, the cross reacting substance is most likely 1-α hydroxy corticosterone, the demonstrated product of the elasmobranch interrenal gland (Idler and Truscott 1966b; Truscott and Idler 1968), which, as has been shown previously, interacts with other corticosterone antisera (Kime 1977; Hazon and Henderson 1984). Despite the lack of parallelism in this assay, such estimates provide a crude indicator of stress levels, particularly when large excursions are identified. (Corticosterone was assayed because the 1-α antiserum was not available to us.) Honn and Chavin (1978) reported that 11.5% of the 1-α-hydroxycorticosterone reacted with antiserum to corticosterone, and that 100% of elasmobranch corticosterone reacted with corticosterone antisera. Respectively, the intra- and inter-assay coefficients of variation ranged from 4 to 11% and from 12 to 15% respectively for our usual nonhuman primate pools or rat pools (corticosterone) run in parallel with the shark samples.

E. Statisical Analyses

Our sample size was limited to between 1 and 10 samples per group. Mean and standard errors of mean (± SEM) were calculated for sample sizes greater than 3. Single samples were noted as such.

Results

A. Immature Female Sharks (Table 1)

1. 17-β Estradiol (E_2)—The predominant serum estrogen in the immature female lemon shark was E_2, with a mean level of 74 pg/mL ($n = 10$). In contrast, E_2 in the immature female tiger shark was 12 pg/mL.

2. Progesterone (P)—P levels in immature female lemon sharks were relatively high compared to those of both mature male lemon sharks and mature females of all species examined (Tables 1 and 2).

3. Testosterone (T) and Dihydrotestosterone (DHT)—Immature female lemon sharks had lower T values than mature female lemon sharks (Tables 1 and 3). Approximately two-fold higher DHT was recorded in immature female lemon sharks (mean 98 pg/mL) compared to T. DHT levels of immature female tiger sharks were lower than those of immature lemon sharks, but, as with the lemon shark, DHT levels were higher than T levels.

Table 1.
Serum steroid hormone concentrations in female sharks in pg/mL. Comparisons between species and levels of maturity.[a] E_2 = 17-β estradiol; P = progesterone; T = testosterone; DHT = dihydrotestosterone; and CS = corticosterone.

Shark species	E_2	P	T	DHT	CS
Immature					
Lemon, *Negaprion brevirostris*, $n = 10$					
Mean	74	751	53	98	429
SE	13	332	17	33	88
Range	23–155	129–3,663	1–162	1–339	152–1,084
Tiger, *Galeocerdo cuvier*, $n = 3$					
Mean	12	104	19	34	643
SE	1	15	8	8	199
Range	10–14	102–104	10–36	20–45	356–1,025
Maturing					
Bull, *Carcharhinus leucas*[b], $n = 1$	104	12	121	2	157
Lemon, $n = 1$	263	54	7	8	353
Mature					
Lemon, $n = 4$					
non-mating	1,030	118	153	82	221
courtship phase	1,382	154	246	148	240
active courtship phase	2,921	138	800	111	456
postpartum	892	216	585	128	1,019
Great hammerhead, *Sphyrna mokarran*[b], $n = 2$	635	2	128	38	124
	1,195	nd[c]	243	135	108
Scalloped hammerhead, *Sphyrna lewini*[b], $n = 1$	1,062	4	295	87	290
Sharpnose, *Rhizoprionodon porosus* (with embryos), $n = 6$					
Mean	2,793	85	39	18	826
SE	506	25	8	—	316
Range	1,248–4,499	14–180	19–69	nd–28	104–2,060
Blacknose, *Carcharhinus acronotus* (with large ova in ovary), $n = 4$					
Mean	823	87	414	15	261
SE	253	14	160	5	27
Range	381–1,364	56–119	48–780	10–25	211–333
Blacktip, *Carcharhinus limbatus* (reproductively quiescent), $n = 3$					
Mean	35	120	16	5	179
SE	—	26	—	—	46
Range	nd–65	80–168	nd–26	nd–5	211–333
Reef, *Carcharhinus perezi* (reproductively quiescent), $n = 4$					
Mean	8	46	9	nd	79
SE	3	12	6	—	8
Range	2–12	10–65	3–22	—	68–103
Nurse, *Ginglymostoma cirratum*[b], $n = 1$	169	193	19	nd	31

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[a] Maturity is based on size (PCL) and other criteria such as calcification of claspers and condition of the ovaries per L. Compagno (1984). See also text for other criteria.

[b] Tournament sample or recently dead animal.

[c] nd = below the level of detectability by RIA method.

Immature female lemon sharks had higher T values than either immature female tiger sharks or mature female nurse, reef, sharpnose, and most blacktip sharks (Tables 1 and 4).

4. Corticosterone (CS)—CS concentrations of immature female lemon sharks varied from 152 to 1084 pg/mL but were within the range for mature female sharks of various species.

B. Immature Male Sharks (Table 2)

1. 17-β Estradiol (E_2)—Immature male, female and mature male lemon sharks had similar E_2 levels.

Table 2.
Serum steroid hormone levels in male sharks in pg/mL. E_2 = 17-β estradiol; P = progesterone; T = testosterone; DHT = dihydrotestosterone; and CS = corticosterone.

Shark species	E_2	P	T	DHT	CS
Immature					
Lemon, *n* = 9					
Mean	89	158	1,398	94	523
SE	35	24	545	41	87
Range	21-347	51-963	128-5,060	9-305	153-903
Tiger, *n* = 3					
Mean	17	695	3,665	896	1,065
SE	7	199	1,237	265	180
Range	9-30	324-1,005	1,756-5,980	400-1,279	837-1,420
Mature					
Lemon[a], *n* = 2	46	174	73,860	3,600	1,650
	10	164	23,320	534	872
Sandbar shark, *Carcharhinus plumbeus*[a], *n* = 1	20	712	73,290	3,920	1,647
Bull, *n* = 2	9	1,176	2,737	156	1,069
	25	4,006	357,540	168,880	3,896
Blacknose, *n* = 2	20	2,582	69,039	10,045	953
	51	5,088	78,455	6,088	925
Reef, *n* = 5					
Mean	6	76	1,562	300	301
SE	2	36	447	170	58
Range	1-11	27-214	853-3,086	77-965	178-505
Blacktip, *n* = 1	11	2,467	25,047	1,621	931
Sharpnose, *n* = 1	269	2,897	40,998	4,680	748
Great hammerhead[a], *n* = 2	21	6,777	59,690	1,680	2,158
	13	311	42,220	626	1,436
Scalloped hammerhead[a], *n* = 1	18	3,638	40,360	9,120	1,657
Nurse[a], *n* = 2	9	64	8,066	1,030	561
	3	48	10,003	546	421

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[a] Tournament samples.

Table 3.
Serum estradiol and testosterone in mature female sharks.

	Estradiol (pg/mL)		Testosterone (pg/mL)	
Shark species	Range	Mean	Range	Mean
Group I	381-4499 pg/mL		48-800 pg/mL	
Lemon	1030-2931	1777.6	153-800	446
Blacknose	381-1364	822.8	48-780	414
Hammerhead	635-1195	964	128-295	222
Lemon[a]	892		585	
Sharpnose	1248-4499	2792.8	19-69	38.2
Group II	2-65 pg/mL		3-26 pg/mL	
Blacktip	4-65	34.5	6-26	16
Reef	2-12	7.7	3-22	9.3
Nurse	169		19	

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[a] Lemon shark female, postpartum.

2. Progesterone (P)—P levels of immature male lemon sharks were lower than those of immature females but within the same range as mature male and female lemon sharks.

P levels of immature male tiger sharks were several-fold higher than those of immature females (Table 2).

3. Testosterone (T) and Dihydrotestosterone (DHT)—An apparent species difference was observed in serum levels of these two androgen hormones. The primary steroid hormone of immature male lemon sharks was T; DHT values were lower. However, tiger sharks had higher levels of both T and DHT than immature lemon sharks: the ratio of DHT/T was 1:15 for the lemon shark and 1:4 for the tiger shark.

4. Corticosterone (CS)—CS levels of immature male lemon sharks were somewhat lower than those of tiger sharks.

Table 4.
Comparison of mature female carcharhinids in various reproductive states in pg/mL. E_2 = 17-β estradiol; P = progesterone; T = testosterone; DHT = dihydrotestosterone; and CS = corticosterone.

Shark species	E_2	P	T	DHT	CS
Females in active reproductive status					
Sharpnose, *n* = 5 (gravid)					
No. of embryo (length)					
3 pups (21 cm)	2072	53	39	9	104
4 pups (18 cm)	2474	79	48	28	970
1 pup (12.6 cm)	2497	53	19	nd[a]	234
2 pups (19.6 cm)	1248	180	25	nd	1327
6 eggs (ovary)	3967	14	29	nd	262
	4499	128	69	nd	2060
Mean	2792.8	84.5	38.2	18	826.2
SE	506	24.9	7.5		315.5
Range	1248-4499	14-180	19-69	9-28	104-2060
Blacknose, *n* = 4 (ovary condition)					
Several ova	381	56	48	nd	333
3 large ova	403	119	780	25	211
3 large ova	1364	100	559	10	228
Several ova	1143	71	269	10	271
Mean	822.8	86.5	414	15	260.8
SE	252.8	14.1	160	5.1	27.2
Range	381-1364	56-119	48-780	10-25	211-333
Lemon, *n* = 4					
Nonmating	1030	118	153	82	221
Recent mating wounds	1382	154	246	148	240
Recent mating wounds	2921	138	800	111	456
Postpartum	892	216	585	128	1019
Females in nonreproductive status					
Blacktip sharks, *n* = 3					
No ova	nd	168	6	nd	158
Early pregnancy	4	113	nd	5	114
No large ova	65	80	26	nd	266
Mean	34.5	120.3	16	5	179.3
SE		26.1			46.0
Range	4-65	80-168	6-26		114-266
6 large ova in ovary	370	4880	858	152	460
Nurse shark, *n* = 1	169	193	19	nd	31
Reef sharks, *n* = 4					
no sizable ova in ovaries or	9	59	3	nd	74
embryos in uterus	12	48	3	nd	103
	nd	65	22	nd	72
	2	10	nd	nd	68
Mean	7.7	45.5	9.3	nd	79.3
SE	3.02	12.3	6.4		8.0
Range	2-12	10-65	3-22		68-103

[a] nd = below the level of detectability by RIA method.

C. Mature Male Sharks

Because mature male sharks were not commonly caught, most data sets contain only 1-3 samples. Only two samples were collected from mature male lemon sharks. However, serum samples were obtained from males of 9 species of carcharhinoid sharks.

1. **Progesterone (P)**—P levels of mature male lemon, reef, and nurse sharks were relatively low compared to those of mature bull, blacknose, blacktip, sharpnose, and hammerhead. In addition the latter 5 species demonstrated concurrently high serum T and DHT levels (Table 2).

2. **Testosterone (T)**—T values were higher in male than

in female sharks, ranging from 853 to 358,000 pg/mL. However, T values of mature male reef and nurse sharks were similar to the relatively low values recorded in immature male lemon sharks.

T values of male lemon, bull, hammerhead, blacknose, sandbar, blacktip, and sharpnose sharks ranged from 23 to 78.5 ng/mL, with the exception of one adult male bull shark whose serum T levels exceeded 350 ng/mL. In the two mature male lemon sharks, T levels averaged 49.0 ng/mL, about 20-fold higher, than those of immature male lemon sharks. Such high T concentrations were accompanied by moderate CS and low P levels. The one bull shark with unusually high T had only moderately elevated P levels, similar to P levels in two of the hammerhead sharks.

3. Corticosterone (CS)—Compared to other sharks, mature male bull, hammerhead, and sandbar sharks had moderately high P and CS levels. In the one bull shark with very high T, CS levels were also the highest. However, the CS/T ratio of this shark was actually lower than that of the male hammerhead sharks.

D. Mature Female Sharks

1. 17-β Estradiol (E_2) (Tables 1 and 3)—Based on serum E_2 levels the mature carcharhinoid female sharks can be sudivided into two groups: those with relatively low E_2 levels between 2 and 65 pg/mL such as reef and most blacktip; and those with higher E_2 levels (between 381 and 4499 pg/mL) such as lemon, blacknose, sharpnose, and hammerheads. The samples from sharpnose, blacknose, and lemon sharks were more complete and included serum from several conspecifics. In addition, it was possible to assess their reproductive condition based on external signs of courtship or ripeness of their gonads. Thus samples were obtained from female lemon sharks during active courtship as evidenced by fresh mating scars, from the sharpnose sharks during mid to late pregnancy, and from blacknose sharks during the ovulatory period. Morphological data indicated two out of three female hammerheads sampled had large ova in the ovary. In contrast, the ovaries of the reef sharks were devoid of any large ova and the oviducts were empty. The female blacktips showed little evidence of reproductive activity with the noteworthy exception of a single mature female with fresh mating scars. This female had a serum E_2 level of 370 pg/mL and had unusually high P levels, exhibiting an unusual serum steroid hormone profile (Tables 3 and 4).

a. Lemon—Mature female lemon sharks had elevated E_2 levels relative to those of immature females. Intermediate levels were noted for one subadult lemon shark (Table 1). High E_2 levels were correlated with high T, but P levels were not correlated with T or E_2 levels.

b. Sharpnose—E_2 levels in the mature sharpnose sharks were comparable to those of mature lemons and somewhat higher than those of the blacknose and the two species of hammerhead. Both P and T levels were relatively low (Table 4).

c. Blacknose—In mature female blacknose sharks E_2 levels were lower than those of lemon and sharpnose, ranging from 381 to 1364 pg/mL, but still relatively high compared to those of blacktip and reef females. P levels were relatvely low and T levels high (Table 4).

2. Testosterone (T) and Dihydrotestosterone (DHT)—Mature female nurse, reef, sharpnose, and most blacktip sharks had lower T levels than immature female lemon sharks (Table 1 and Table 4). However, elevated T and E_2 levels were observed in mature female lemon, blacknose, hammerhead sharks, and one specimen of blacktip shark (Tables 1, 3, and 4). In reproductively active and postpartum lemon sharks, T levels were several-fold greater than those in immature female lemon sharks. The maximum values for serum T among mature female sharks were 800 pg/mL in the courtship phase shark vs. 585 pg/mL for a lemon shark that had just given birth. Concurrent with relatively high E_2 levels in both species of adult female hammerhead sharks, T values were also high (Table 1).

Dihydrotestosterone levels were low and did not appear to increase concurrently with T (Tables 1 and 4).

3. Progesterone (P)—Serum P levels were generally low in all species of mature female sharks, when compared to mature males, immatures, and other vertebrates in general (Tables 1 and 2).

Three exceptions to this generality were observed: One reproductively active nurse shark had a relatively high progesterone level of 193 pg/mL (Table 1); one postpartum lemon shark had slightly elevated P (216 pg/mL) (Table 1); and the third exception was the single reproductively active female blacktip with extensive and recent mating wounds. The serum P level of this shark was 40 times higher (4,880 pg/mL) than that of any other female shark we measured. Most noteworthy were the concomitant high testosterone (858 pg/mL) and estradiol (370 pg/mL) levels.

4. Corticosterone (CS)—Several instances of simultaneous progesterone and corticosterone elevations were observed among mature female sharks. In the twenty-five female sharks studied, three had elevated CS: a postpartum lemon shark, and two of the 6 sharpnose sharks (Table 1).

E. Mature Female Lemon Shark: Chronically, Multiple-Sampled Animal

Table 5 lists the serum steroid hormone levels measured in a wild mature female lemon shark briefly held in captivity and sampled over a period of six days. This shark had recent mating scars and so was considered by us as

Table 5.
Stress-related steroid serum hormone levels (pg/mL) in chronically sampled animals.

	Estradiol	Progesterone	Testosterone	Corticosterone
Mature female lemon shark with fresh mating scars, $n = 1$				
Day 1	2921	138	800	456
Day 2	2238	121	262	338
Day 3	806	70	78	207
Day 4	600	50	69	125
Day 5	809	70	88	130
Mature male nurse shark, $n = 1$				
Day 1–AM		200	15,860	1036
PM		156	9,390	875
Day 2–AM		132	7,660	717
PM		110	7,250	723
Day 3–AM		74	5,220	598
PM		51	4,550	519
Day 4–AM		76	4,720	816
PM		22	3,640	471
Day 5–AM		34	3,360	540

reproductively active. A similarly captive mature male nurse shark was also sampled. In both sharks all four serum steroid hormone levels declined continuously over several days until the fifth and last day when values began to rise slightly in both animals.

Discussion

The purpose of this study was to measure serum levels of circulating steroids in the placental sharks. To our knowledge such measurements are currently unavailable. Because our long-term goal is to understand the reproductive cycle of the lemon shark, we tried to make our measurements at a time when this species was actively courting and bearing young. In addition, we took samples from immature specimens to reveal any ontogenetic changes in amounts of circulating steroids. Finally, we collected information from a variety of placental carcharhinoids for comparative purposes.

Throughout the study, we attempted to correlate steroid levels with the reproductive state of the specimen. We used morphological data such as size and state of ovaries and testis, size and calification of claspers, and total length, as well as external signs such as fresh mating scars to determine maturity. We also evaluated the oviducts and cloaca for signs of pregnancy or copulation. Near term gravid females were easy to distinguish because of their expanded abdomen. The result was a series of qualitative and quantitative observations leading to an estimation of the reproductive condition of each specimen.

The hormonal levels were strictly quantitative, but owing to the difficulty of capturing large numbers of mature specimens of various species, we were required in some cases to base our discussion on serum samples from a single specimen. Therefore, we did not distinguish between individual and species differences (except with immature sharks), but rather reported ranges of hormone levels in the eleven species investigated. Our results allow us to compare ontogenetic changes, sex differences, and reproductive state differences among carcharhinoid sharks. However, the paucity of multiple data from individual animals and the lack of seasonal data (our samples were taken only in spring and fall 1987) preclude any discussion of individual differences and only allow us to make suggestions, but not definite conclusions, concerning the functioning of the reproductive cycles.

We are aware that the measurement of steroid hormones in the serum does not describe their biological functions, but in our long-term, ongoing study of the Carcharhinoidea, this measurement is a necessary first step to understanding hormonal roles in reproductive biology. We can tentatively say that in female placental sharks both E_2 and T appear to play a role in reproduction and that male sharks generally have high serum T levels. Our data from chronically sampled sharks suggest that short-term captivity affects the physiological status of the animal, resulting in reduced serum levels of reproductive hormones. The correlation of hormone levels with reproductive conditions leads us to believe that sophisticated cycles may be functioning in the reproduction of the viviparous, placental elasmobranchs.

E_2 in Female Carcharhinoid Sharks

The low but measurable estradiol levels in immature female lemon sharks, which increased with maturity, suggest that this hormone plays a role in reproductive maturation and may regulate reproductive cycles in adults.

The level of E_2 in mature female sharks may be related to their reproductive condition. The sharks in the high serum E_2 group were reproductively active, either approaching or in the breeding stage as indicated by several lines of gross anatomical evidence (such as large, well-rounded ovaries with mature or maturing ova), or in either a differentiating or expecting uterine stage, or in a postpartum state. The female sharks in the high E_2 group included the lemon, hammmerhead, blacknose, and sharpnose sharks. Specifically, the lemon sharks were either in a ripe ovarian or a postpartum stage, the hammerheads were either in ripening or in ripe ovarian stage, the blacknoses had large ova in the ovary, and the sharpnoses had formed embryos of about half-term. In contrast, female blacktip and reef sharks with low estradiol appeared to be in a quiescent sexual stage as suggested by lack of mating scars, lack of pregnancy, and by varying sizes of ova in the ovary.

Studies of the oviparous shark, *Scyliorhinus canicula*, reported E_2 ranges from 5 to 40 ng/mL, with simultaneous elevations of E_2 and T levels during periods of peak egg laying (Sumpter and Dodd 1979; Jenkins and Dodd 1982). Recently, Koob et al. (1986) reporting on the skate found good correlation between 17-β estradiol levels and advancing follicular development. Our measured elevations in E_2 during active reproduction suggest that similar events may be occurring in the female carcharhinoid sharks.

T in Female Carcharhinoid Sharks

High testosterone levels were found concurrently with high estradiol levels in reproductively active and postpartum lemon sharks, blacknoses with large ovarian eggs, and 2 of 3 hammerheads. In contrast, gravid sharpnose sharks had low serum T, although E_2 levels were high. These observations lead us to believe that in placental sharks, T may function in courtship, ovulation, and after parturition but may be of less importance during pregnancy.

Similar patterns with E_2 and T have been observed in other elasmobranchs. In the oviparous shark, *S. canicula*, E_2 varied from 5 to 40 ng/mL while plasma T was high all year, varying from 1 to 8 ng/mL, with levels rising during the peak egg-laying season (Jenkins and Dodd 1982). The results of Koob et al. (1986) indicated that T, as well as E_2, are predominant steriods during the follicular stage in the skate *R. erinacea*. Our data from a number of reproductively active female carcharhinid sharks suggest a similar pattern.

T elevations have also been observed among other lower vertebrates such as the Atlantic salmon *Salmo salar*, where T is higher in females than males (Stuart-Kreger et al. 1981). Similarily, in the red-sided garter snake *Thamnophis sirtalis parietalis*, plasma T levels were significantly elevated around the time of ovulation (Whittier et al. 1987). In these cases, increased T apparently signalled ovulation. In the blue cod, *Parapercis colias*, T has been demonstrated to be a precusor of E_2. T levels were usually highest just prior to final oocyte maturation (Pankhurst and Conroy 1987).

P in Female Carcharhinoid Sharks

High progesterone levels in the juvenile female lemon shark may indicate a developmental role for this hormone. Compared to other vertebrates, adult female carcharhinoid sharks have low and stable levels of P. In placental mammals progesterone is periodically elevated at times during pregnancy. In *Squalus acanthias*, P levels remain high throughout pregnancy until near-term and E_2 levels remain low during this period (Tsang and Callard 1984, 1988). The lack of P elevation in two small groups of gravid placental carcharhinids sampled (i.e., the mid-term gravid sharpnose sharks and one very late-term lemon shark) suggests a basic difference in hormonal mechanisms of pregnancy between the requiem and dogfish sharks and between the placental sharks and higher mammals. In other elasmobranchs the corpus luteum produces P (Klosterman and Callard 1986). Determining the source and level of P during the course of fetal development would help in our understanding of the hormonal control of pregnancy in the placental sharks.

Serum P levels were very high in one reproductively active adult female blacktip shark. In this shark, P levels were 40 times higher (4,880 pg/mL) than those of any other female shark and were correlated with high T and E_2 levels. This preovulatory condition appears to be similar to that described for the skate *R. erinacea* by Koob et al. (1986) where plasma P peaked forty-eight hours prior to ovulation and then dropped rapidly.

DHT in Female Carcharhinoid Sharks

In immature female lemon sharks we found serum DHT concentrations even higher than T levels. This is remarkable since in adult female lemon sharks DHT was lower than T while in *S. canicula* DHT levels were neglible (Sumpter and Dodd 1979). This high ratio in immature female lemon sharks is noteworthy because there are only a few examples of high serum DHT:T ratios in vertebrates. One example is the serum of the mature female dove (*Streptopelia risoria*) during certain phases of the courtship cycle (Feder et al. 1977).

E_2 and T in Male Carcharhinoid Sharks

Among immature male sharks, measurable E_2 and T suggest that both hormones may be important in sexual development. The presence of both hormones is not surprising because E_2 is formed by the aromatization of androgens, often as a normal product of the testis, and in the males of diverse species, such as stallions, boars, and mudpuppies, makes up a large proportion of the total testicular steroid secretion (Koob et al. 1986).

T in Male Carcharhinoid Sharks

Among mature male carcharhinoid sharks, several observations are noteworthy: Serum testosterone concentrations had a four hundred-fold range, from 853 pg/mL to 358 ng/mL (358,000 pg/mL). These are wider ranges than previously reported for other elasmobranchs (Idler and Truscott 1966a; Jenkins and Dodd 1982). Even within a single species (i.e., the reef shark), values ranged from 853 pg/mL to 3,100 pg/mL. The nurse and reef shark values were less than 10 ng/mL (10,000 pg/mL). However, with one exception, the rest of the species all demonstrated T levels between 23 and 70 ng/mL, values that are comparable to those reported for the skate, *R. radiata* (Idler and Truscott 1967), and higher than those reported for the lesser spotted dogfish, *S. canicula* (Jenkins and Dodd 1982). The high T levels observed in mature male carcharhinoids may have roles either in sexual behavior and reproductive functions or in stress, as has been demonstrated in guinea pigs (Sachser 1987). Another possibility (Callard et al. 1978) is that hormones in such high levels may not be acting as hormones but rather as precursors for other unidentified steroids such as estrogens.

The value of 358 ng/mL for T, which we measured in one bull shark, is among the highest recorded in vertebrate serum. In breeding male musk turtles, *Sternotherus odoratus* (Mendonca 1987), male noctule bats, *Nyetalus noctula* (Racey 1982), and Asian bull elephants, *Elephas maximus* in the highly aggressive state of "musth" (Rasmussen 1988), the maximum measured serum concentrations were 68.5, 134, and 127.8 ng/mL, respectively. In male rhesus monkeys, T plays a role in rank determination and affects aggressive behavior (Rose et al. 1971). For comparison, T levels in two teleosts include the breeding *Fundulus heteroclitus* at 11.3 ng/mL (Cochran et al. 1987) and the brown bullhead, *Ictalurus nebulosus*, 1.47–1.65 ng/mL (Rosenblum et al. 1985).

Fletcher et al. (1969) suggested that high levels of T in the skate *Raja radiata* were unrelated to aggressive behavior. They demonstrated that high circulating levels of T in the plasma of both male and female skates were the result of a low metabolic clearance rate rather than high production.

P in Male Sharks

The source of high progesterone in immature males is debatable. Potentially, as in other elasmobranchs, the testis is one source and has previously been demonstrated to produce P, T, and E in vitro (Callard et al. 1981). However, an assessment of any possible interrenal contribution (Klesch and Sage 1973) would be of interest, especially since in some individual sharks P and CS increase concurrently.

The serum assayed in this study was from sharks collected by several fishing techniques. We were concerned about the varying and unmeasureable degrees of stress and/or stimulation which occurred during catching and sampling. Thus we measured CS as well as P levels to look for correlations between apparent stress and hormone increments. At times concurrent elevations or depressions in serum concentrations of P and CS occurred; however, no consistent pattern was apparent.

Serial Sampling of Serum from a Wild Carcharhinid Shark

A unique aspect of this paper is that we report for the first time the collection of serial samples from a reproductively active, wild, carcharhinid shark held briefly in captivity. Serum steroid levels from this and one other shark initially fell during confinement. We are now attempting to obtain complete records thoroughout the breeding season and the entire year on mature adult lemon sharks to help separate out seasonal, species, and individual variation. Our ongoing field work focuses on reproductively active female sharks. We will look for cyclic changes reminiscent of mammalian estrous cycles, such as concurrent elevations in E and P, spikes in P levels, or simultaneous rises in E and T levels. Important biological roles in maturation and in cycling have been described for androgens in female mammals (Givens 1978; Young Lai 1978) and in teleosts (Pankhurst and Conroy 1987). Androgens may possibly have similar functional roles in female carcharhinid sharks.

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Elasmobranch Age Determination and Verification: An Updated Review

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ABSTRACT

Growth curves for elasmobranchs have generally been derived from age estimates based upon opaque and translucent bands in calcified structures such as vertebrae and fin spines. In the past, few studies have attempted to determine the temporal periodicity of band deposition. The various methods used to estimate age and verify the periodicity of growth zones in elasmobranchs include 1) back calculation and calculation of growth model parameters (neither of which strictly qualifies as verification); 2) size frequency analysis; 3) centrum or spine edge dimensions, histological characteristics, and/or elemental microanalysis; 4) radiometric dating; 5) laboratory growth studies; 6) tag recapture results from the field; and 7) tetracycline marking in both laboratory and field studies. Since the last (1986) review, there have been at least 42 studies initiated, 19 of which are in progress and 23 of which are published, addressing age verification in 39 species of elasmobranchs. To date, six species have such poorly calcified vertebrae that no existing methodology is useful for age determination. One species has calcified structures which do not exhibit predictable growth zones. Another 39 species studied have partially verified growth zones in their calcified structures. There are sufficient data to validate the growth zones in only six species. The use of multiple techniques in recent studies is promising, and should be encouraged in future studies. It will still be important in future growth studies to stress the physiological aspects of calcium dynamics and regulation.

Introduction

Holden (1974) proposed that elasmobranchs had life histories which would make them particularly susceptible to overfishing. He listed von Bertalanffy growth model parameters for several species that had been studied using techniques available to that date. More recently, increasing fisheries for elasmobranchs have stimulated more biologists to study aspects of their life histories, including age, growth, and reproduction.

In most cases, Holden's (1974) growth parameters were predicted by indirect evidence, including body size at conception and birth, length of the gestation period, and maximum observed body size. In a few cases, however, he had information on age and growth which was estimated from growth zones (also called bands or rings; see Cailliet et al. 1983, 1986a) in calcified structures such as spines and vertebral centra. But, there still remained the problem of demonstrating that these growth zones were deposited annually.

Since then, additional techniques have been developed to facilitate the counting of opaque and translucent zones (Cailliet et al. 1983). However, as pointed out in the most recent review (Cailliet et al. 1986a), few elasmobranch growth studies had evaluated the temporal periodicity of band or ring deposition in spines and vertebral centra. This lack of information was apparently typical of many fish age and growth studies to that date and had hampered fishery scientists from obtaining an accurate and clear understanding of the growth processes that these zones represented (Beamish and McFarlane 1983).

Several authors have attempted to define the process by which growth zone deposition in fishes can be evaluated (Brothers 1983; Jearld 1983; Wilson et al. 1983). The term "verification" is defined in most dictionaries as the process of ascertaining the truth, while "validation" is proving something to be soundly founded on fact, and thus true. Cailliet et al. (1986a) proposed to redefine verification as "a process of evaluating an assumption, which can only be validated when that process is complete." With respect to age determination, verification can be more specifically defined as the process of confirming an age estimate by comparison with other indeterminate methods. Cailliet et al. (1986a) further defined age validation as "the conclusion, after sufficiently testing hypotheses about the temporal periodicity of band deposition, that bands counted are deposited predictably.'' Validation therefore requires proving the accuracy of an age estimate by comparison with a determinate method, and this procedure must be completed for all age classes available, to strictly follow the requirements outlined by Beamish and McFarlane (1983).

Cailliet et al. (1986a) then organized verification procedures into four general categories, which included seven specific methods: 1) analysis of growth model parameters derived from band counts, including back calculation (neither of which strictly qualifies as verification); 2) size frequency analysis; 3) centrum or spine edge dimension, histological characteristic, and/or elemental composition analysis; 4) radiometric dating; 5) laboratory growth studies; 6) tag-recapture growth from the field; and 7) tetracycline marking in both laboratory and field studies.

It is the objective of this paper to update the 1986 review and include new or previously overlooked studies that have attempted to verify and/or validate the timing of growth zone deposition in elasmobranch calcified structures. In reviewing these recent studies, I will characterize the approaches and combinations of approaches that various authors have taken to achieve the ultimate objective of age validation. Finally, I will tabulate those taxa for which age and growth studies have been unverified, verified, or validated.

Verification and Validation Studies

Back Calculation and Growth Model Parameters

When no other verification procedures are possible, one can use growth model parameters, such as those derived from the von Bertalanffy growth equation (Holden 1974), as a qualitative evaluation of how well a calculated curve fits known size information, such as length at birth and maximum observed length. However, this growth equation provides only rough comparative values and does not serve as a true test of the annual periodicity of band formation. Also, as pointed out by Pratt (1990), accurate predictions of life history parameters using Holden's (1974) method seldom are accurate. Nevertheless, this approach has been recently used for *Triakis semifasciata* (Kusher 1987; Kusher et al., In prep.), *Mustelus henlei* and *M. californicus* (Yudin 1987; Yudin and Cailliet 1990), and *Myliobatis californica* (Martin and Cailliet 1988). In all three cases, growth parameter information was used in conjunction with other evidence.

Growth curves can also be developed from back-calculated estimates of size at previous ages, which are in turn derived from measurements of the zones of calcified structures from larger (and presumably older) individuals. When these back-calculated curves are compared with those from other methods, they provide only a check on the growth model used, and are actually more useful for providing data on sizes of missing age classes and for evaluating changes in size at age over past time periods.

This technique has been popular in 11 recent studies of rajiform, myliobatidiform, and carcharhiniform elasmobranchs. Back-calculated growth curves were presented by Ryland and Ajayi (1984) for three species of skates (*Raja clavata*, *R. microocellata*, and *R. montagui*), Martin and Cailliet (1988) for *Myliobatis californica*, and Tanaka (1987) for *Dasyatis garouensis*. Back calculations were used by Yudin (1987) and Yudin and Cailliet (1990) on *Mustelus henlei* and *M. californicus*; Schwartz (1984) on *Carcharhinus acronotus*; Killam (1987) and Killam and Parsons (In press) on *C. limbatus*; and Branstetter (1987a,b,c), Branstetter et al. (1987), and Branstetter and Stiles (1987) on a combination of carchariniform sharks, including *C. brevipinna*, *C. falciformis*, *C. leucas*, *C. limbatus*, *Galeocerdo cuvieri*, *Rhizoprionodon terraenovae*, and *Sphyrna lewini*. In most of these cases, back calculation was used in conjunction with other techniques.

Size Frequency Analysis

Despite the difficulties associated with using size frequency analysis, it is often possible, especially with smaller, younger size classes, to trace modes of sizes over time and to compare the rates derived from this procedure with growth curves generated by another method. This approach has been recently used successfully for age verification by Brander and Palmer (1985) on *Raja clavata*; Smith and Merriner (1987) on *Rhinoptera bonasus*; Martin and Cailliet (1988) on *Myliobatis californica*; Kusher (1987) and Kusher et al. (In prep.) on young *Triakis semifasciata*, Tanaka (Faculty of Mar. Sci. and Tech., Tokai Univ., Japan, pers. commun., 1986) on *Lamna ditropis*; Tanaka (1984), Skomal (1987) and Skomal et al. (1988) on *Prionace glauca*; and Killam (1987) and Killam and Parsons (In press) on *Carcharhinus limbatus*. Saiko and Yoshimura (1985) and Yoshimura and Kawasaki (1985) plotted the size of embryonic *Carcharhinus longimanus* and young *C. falciformis*, respectively, but did not compare the size modes with the growth curves they developed from vertebral centrum band counts. Natanson and Cailliet (In press) were not successful using commercial catch data in discerning size modes for *Squatina californica* off Santa Barbara, California.

Centrum Edge Analysis

One useful and fairly direct verification technique is to monitor the width and density of the centrum edge over time in many different individuals and to discern changes which might be seasonal. This approach includes categorizing the edge as translucent or opaque (Wilson et al. 1983), measuring and/or grading band widths, and analyzing the actual levels of calcium and phosphorus at the edge using x-ray or electron microprobe spectrometry (Cailliet and Radtke 1987). There have been 17 recent studies using centrum edge analysis on rays and sharks. For rays, this technique was used by Lessa (1982) on *Rhinobatos horkelii*; Roussouw (1984) on *R. annulatus*; Martin and Cailliet (1988) on *Myliobatis californica*; Schmid (1987) on *Dasyatis sabina*; and Tanaka (1987) on *D. garouensis*. For sharks, it was used by Kusher (1987) and Kusher et al. (In prep.) on *Triakis semifasciata*; Yudin (1987) and Yudin and Cailliet (1990) on *Mustelus henlei* and *M. californicus*; Killam (1987) and Killam and Parsons (In press) on *Carcharhinus limbatus*; Tanaka (pers. commun.) on *Lamna ditropis*; Tanaka (1984), Skomal (1987), and Skomal et al. (1988) on *Prionace glauca*; and Branstetter (1987a,c), Branstetter et al. (1987), and Branstetter and Stiles (1987) on a combination of carchariniform sharks, including *Carcharhinus brevipinna*, *C. leucas*, *C. falciformis*, *C. limbatus*, *Galeocerdo cuvieri*, *Rhizoprionodon terraenovae*, and *Sphyrna lewini*. Centrum edge analysis was also used on *Sphyrna lewini* in Taiwan by Chen and Lo (1988). Natanson and Cailliet (In press) could not detect any seasonal periodicity in centrum edge characteristics using histology of centra from *Squatina californica*.

The microanalysis of calcium and phosphorus across a vertebral centrum or at its edge has only been used once since this technique was introduced and tested for elasmobranchs by Cailliet et al. (1986a) and Cailliet and Radtke (1987). Carrier and Radtke (1988) have used electron microprobe analyses on recaptured nurse sharks, *Ginglymostoma cirratum*, which had been injected with tetracycline.

Radiometric Dating

This technique uses relative radioactivity levels of naturally occurring isotopes from different parts of a vertebral centrum to estimate age. It was not completely successful when attempted for four species off California (Welden et al. 1987). Radiometric age estimates for *Carcharodon carcharias* and *Squatina californica* roughly agreed with those from other age determination studies. However, for *Triakis semifasciata* and *Alopias vulpinus*, radiometric age estimates were too variable and could not be used for verification. This was most likely due to violation of the two inherent assumptions of this technique: constant incorporation of the radionuclide being measured, and no loss or gain except by radioactive decay. It appears that elasmobranchs may resorb or remodel their calcified structures and thus violate these assumptions. Perhaps for these reasons, and the technical, time-consuming, and expensive methodology, no other attempt at applying the radiometric dating technique has been made on elasmobranch fishes.

Laboratory Growth Studies

The use of this approach for age verification has increased since the Cailliet et al. (1986a) review. There have been six new or previously undiscovered studies which used captive growth information to predict natural growth in the field. McLaughlin and O'Gower (1971) had used this technique on *Heterodontus galeatus*. Laboratory growth studies since the 1986 review include Yoshimura and Kawasaki (1985) on small *Carcharhinus falciformis*; Branstetter (1987a,b) on *C. limbatus*, *C. plumbeus*, and *Rhizoprionodon terraenovae*; Parsons (1987) on *Sphyrna tiburo*; Taylor and Wisner (1990) on *Carcharhinus melanopterus*; and Van Dykhuizen and Nygren (1987) on *Notorhynchus cepedianus*.

Field Growth Studies

The difficulty of recapturing tagged elasmobranchs, which have been at large a sufficient amount of time for significant growth to have occurred, has most likely prevented this approach toward age verification from being very productive. In two situations, however, localized populations of *Ginglymostoma cirratum* (Carrier 1987) and *Dasyatis sabina* (Schmid 1988) were tagged and the information available upon recapture was effectively used to verify growth rates. Also, the extensive shark tagging program on the east coast has produced some useful tag-recapture information on *Prionace glauca* (Skomal 1987; Skomal et al. 1988).

Laboratory and Field Growth with Tetracycline

According to Beamish and McFarlane (1983), the combination of known growth with tetracycline injection is essential to any age validation study. This approach provides somatic growth information along with a discrete mark in the calcified structure, which enables a direct comparison of growth zone deposition with time at liberty (Smith 1984). The direct nature of this approach has made it popular, despite the problems associated with laboratory growth and the low probability of recapturing organisms that have been in the wild a sufficient amount of time. Selection of dosages of tetracycline for use in such studies has been evaluated by McFarlane and Beamish (1987a).

Since the Cailliet et al. (1986a) review, there have been five laboratory studies in which tetracycline was used as a marker to discern growth zone formation, subsequent to tetracycline injection, on individuals which had either been sacrificed or which had died naturally in captivity. Brown and Gruber (1986) reported growth rates and band deposition patterns for *Negaprion brevirostris* grown under laboratory conditions. Branstetter (1987b) provided growth information for neonate *Rhizoprionodon terraenovae*, *Carcharhinus plumbeus*, and *C. limbatus* grown under laboratory conditions. Cailliet et al. (1986b) opportunistically studied growth of whale sharks, *Rhincodon typus*, which had been kept in captivity in the Okinawa Expo Aquarium. One of these had been fed food laced with tetracycline several times, over more than a year's period. The preliminary results of this study indicated that *R. typus* deposits one pair of growth zones per year in captivity. Luer and Cailliet (In prep.) are presently studying laboratory reared *Raja eglanteria*, half of which were injected with tetracycline and the other half not. Natanson and Cailliet (In press) maintained three *Squatina californica* juveniles for up to one year in laboratory conditions and found that bands were deposited in their vertebral centra as a result of somatic growth rather than as a result of any predictable seasonal, annual, or other temporal phenomena.

Six additional field studies have been initiated or published in which tetracycline was used as a marker to discern and verify growth zone formation. In these studies, individuals were recaptured after a sufficient period of time to detect growth. Three of these studies (Beamish and McFarlane 1985; Tucker 1985; McFarlane and Beamish 1987b) validated annual deposition of growth zones in spine sections of the spiny dogfish, *Squalus acanthias*. These studies were on individuals of multiple size classes and over many years at liberty. Parsons (1987) combined tag-recapture and tetracycline to document growth in centra of *Rhizoprionodon terraenovae* in Florida. Kusher et al. (In prep.) received information on growth from *Triakis semifasciata* which had been tagged, injected with tetracycline, released, and set at large off central California for 1 to 7 + years. Skomal et al. (1988) used a similar approach in studying *Prionace glauca* field growth in the western Atlantic. Natanson and Cailliet (In press) studied centra from six field-tagged, recaptured *Squatina californica*, and found variable growth rates, tetracycline uptake, and subsequent band deposition patterns. None of the results on *Squatina californica* supported the annual band pair deposition hypothesis.

Present Status of Verification and Validation Studies

Species with Poorly Calcified Structures

The vertebral centra of at least six species have been determined to be too poorly calcified to provide useful growth information (Cailliet et al. 1983). These represent either relatively primitive families or species which inhabit deep water and include *Notorhynchus cepedianus*, *Hexanchus griseus*, *Echinorhinus cookei*, *Somniosus pacificus*, *Apristurus brunneus*, and *Parmaturus xaniurus*. It is not known for sure what causes this lack of calcification. It might be due to the primitive systematic position of the groups or a secondary adaptation to the deep sea environment, which is dark, cold, perhaps low in calcium, and food-poor. A more comprehensive survey of these families and of deep-dwelling elasmobranchs from normally shallow-dwelling families is necessary to better understand the reasons for poor calcification.

Species with Well Calcified Structures: Age Not Verified

No matter what technique is followed, one species (*Squatina californica*) remains an enigma (Natanson and Cailliet, In press). They are born with 6 to 7 bands in their vertebral centra, growth curves based on size and band counts are atypical, centrum edge histology and size frequency analysis are inconclusive, and both laboratory grown and field-tagged, tetracyline-injected returns provide no reasonable periodic basis for band deposition. This species may deposit calcified zones in its vertebrae only when somatic growth is occurring rapidly. It would be interesting to see what growth characteristics are typical of other species of this genus.

Species with Well Calcified Structures: Age Partially Verified

From this study and past reviews of the literature (Cailliet et al. 1983, 1986a), a total of 39 species of elasmobranchs have had one or more verification studies performed using calcified structures (Table 1). This includes seven species of skates in the family Rajidae, six species of rays in the families Dasyatididae, Myliobatididae, and Rhinobatidae, and 25 species of sharks, including members of the families Squalidae, Heterodontidae, Gingylmostomatidae, Rhincodontidae, Alopiidae, Cetorhinidae, Lamnidae, Triakidae, Carcharhinidae, and Sphyrnidae.

All indications are that analysis of the growth zone formation in calcified structures of these species will eventually conform to the hypothesis that they have an annually formed pair of opaque and translucent bands. Because in most cases, this prediction is based upon only one or two corroborating studies, this hypothesis will have to be seriously tested for these and the other numerous species of elasmobranchs worldwide, using a combination of approaches. Size frequency analysis and centrum edge analysis have been used on most species, while laboratory and field growth, calcium microanalysis, and radiometric dating have been less commonly applied.

Species with Well Calcified Structures: Age Validated

To date, the temporal periodicity of calcified growth zones has been validated for only six species of elasmobranch (Table 2). Perhaps the best studied species are those which used several approaches on *Negaprion brevirostris* (Gruber and Stout 1983; Brown and Gruber 1986; Pike and Gruber 1988), *Rhizoprionodon terraenovae* (Branstetter 1987b; Parsons 1985), and *Triakis semifasciata* (Smith 1984; Kusher 1987; Kusher et al., In prep.). Their methods include size frequency analysis, centrum edge analysis, and both laboratory and field growth using tag-recapture techniques and

Table 1.
Elasmobranch species with age and growth partially verified. Information based on references cited in Cailliet et al. (1986a) and this paper. X indicates verification; (X) indicates an ongoing, unpublished, or incomplete verification study.

	Verification technique						
Species	Size frequency analysis	Centrum edge analysis	Lab growth	Field growth	Radiometric dating	Calcium microanalysis	Back calculation
Notorhynchus cepedianus			(X)				
Gingylostoma cirratum				(X)		(X)	
Rhincodon typus			(X)				
Heterodontus galeatus			X				
Alopias vulpinus	X				(X)	X	
Carcharodon carcharias					(X)		X
Isurus oxyrinchus	X			X			X
Lamna ditropis	(X)	(X)					
L. nasus	X						
Galeorhinus australis	X			X			
Mustelus californicus		X					X
M. henlei		X					X
M. manazo		X					
Carcharhinus acronotus							X
C. amblyrhynchos			X	X		X	
C. brevipinna		X					X
C. falciformis		X	X				X
C. galapagensis				X			
C. leucas		X		X			X
C. limbatus	(X)	X	X				X
C. longimanus	(X)						
C. melanopterus			(X)				
C. obscurus							X
Prionace glauca	X	X		(X)			
Galeocerdo cuvieri		X					X
Sphyrna lewini		X					X
S. tiburo			(X)				
Dasyatis garouensis		X					X
D. sabina		X		X			
Myliobatis californica	X	X					X
Rhinobatos annulatus		X					
R. horkelii		X					
Rhinoptera bonasus	X	(X)					
Raja brachyura				X			
R. eglanteria	X		(X)				
R. erinacea		X					
R. fusca	X	X					
R. microocellata							*X*
R. montagui				X			X
39 species	12 spp.	19 spp.	9 spp.	10 spp.	2 spp.	3 spp.	16 spp.

tetracycline marks for *N. brevirostris* and *R. terraenovae*, and all of these approaches except laboratory growth for *T. semifasciata*. Evidence also supports annual deposition of growth zones in vertebral centra of *Raja clavata* (Ryland and Ajayi 1984; Brander and Palmer 1985), *Carcharhinus plumbeus* (Casey et al. 1985; Branstetter 1987b), and *Squalus acanthias* (Beamish and McFarlane 1985; Tucker 1985; McFarlane and Beamish 1987).

Discussion

It is obvious from an analysis of the literature reported here that recent researchers have been heeding Beamish and McFarlane's (1983) warning by using multiple methods (e.g., Pratt and Casey 1983) and attempting marking studies both in the laboratory and field. Of the 42 studies on 39 total elasmobranch species initiated since the 1986

Table 2.
Elasmobranch species with age and growth validated. X indicates verification; (X) indicates ongoing unpublished or incomplete verification study.

	Verification technique						
Species	OTC mark	Field growth	(and/or)	Lab growth	Centrum edge	Size frequency	Information based on
Negaprion brevirostris	X	X		X			Gruber and Stout 1983 Brown and Gruber 1986 Pike and Gruber 1988
Triakis semifasciata	X	X			X	X	Smith 1984 Kusher 1987 Kusher et al, In prep.
Squalus acanthias	X	X			X	X	Tucker 1984 Beamish and McFarlane 1985 McFarlane and Beamish 1986
Raja clavata	X	X		(X)		X	Ryland and Ajyi 1984 Brander and Palmer 1985
Rhizoprionodon terraenovae	X	X		X	X	X	Branstetter 1987b Parsons 1985
Carcharhinus plumbeus	X	(X)		X		X	Casey et al. 1985 Branstetter 1987b

review (either in progress (19) or published (23)), 12 have used more than one verification technique on a total of 18 different species. The most common combination of techniques was back calculation and centrum edge analysis, used in six studies on nine species. This was followed by centrum edge analysis and size frequency analysis (4 and 4, respectively), and back calculation, centrum edge analysis, and size frequency analysis (2 and 2).

Single techniques were also used quite commonly. There were six laboratory growth studies, covering six species of elasmobranchs, followed by laboratory growth with tetracycline, and field growth with tetracycline, both of which were represented by four studies and four species. Back calculation alone was used in three studies on five species, while size frequency analysis and centrum edge analysis were used alone in two studies on two species each. The other techniques were used less frequently, usually in only one study.

At the end of the previous review (Cailliet et al. 1986a), recommendations were made for future directions that elasmobranch age and growth studies should take. Nothing has changed since then to radically modify these statements. Rather, there is now even more evidence that species, and even families, differ in their calcium deposition patterns and that the role of endocrine systems in calcium regulation needs to be investigated in much more depth in elasmobranchs, as it is now being actively investigated in bony fishes (Mugiya 1987). Knowledge of calcium metabolism and regulation will help us understand the interplay between ecological and physiological factors and how they sculpt the features of calcified structures, which may reflect the age and growth patterns of elasmobranch fishes.

The relatively large body of literature resulting from studies only in the past few years indicates that there is a great interest in this aspect of the life histories of elasmobranchs. We can only hope that this interest continues and that future investigators maintain the trend toward using multiple techniques to verify and ultimately validate their age and growth estimates for the myriad of elasmobranchs still not studied or poorly understood.

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Growth Characteristics of Two Populations of *Mustelus manazo* from Japan Based upon Cross-Readings of Vertebral Bands

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ABSTRACT

Vertebral centra from *Mustelus manazo*, collected off Nagasaki in southern Japan and from Choshi in the north, were used in a cross-exchange and comparative reading study among three laboratories (two in Japan and one in the United States) to determine if real differences occurred in the growth rates of these two populations. Generally, band counts were similar among techniques and laboratories, but the counts of the U.S. researchers were slightly higher owing to differences in interpretation and criteria of growth zones. Because of relatively low precision and percent agreement, and relatively high variability in size at age, the growth characteristics of the two populations of *M. manazo* cannot be distinguished statistically. The size-at-age estimates were identical within sex and between populations. But the von Bertalanffy growth function did not fit the data well and produced artificially high L_∞ (asymptotic length) estimates in the initial studies, thus suggesting that growth in the two populations was different. A similar exchange of centra from two California species (*Mustelus henlei* and *M. californicus*) produced relatively high precision and percentage agreements, and low error between techniques and laboratories. The interpretation of calcified (opaque) and less calcified (translucent) zones was verified by a comparison between the Japanese sectioned and haematoxylin-stained vertebral centra and those x-radiographed in California. Growth characteristics of the two California species of *Mustelus* studied were similar to those of the Japanese species, with *M. californicus* reaching slightly higher L_∞ values than *M. manazo* or *M. henlei*.

Introduction

The genus *Mustelus* (Family Triakidae), commonly called smoothhounds, has at least 20 species worldwide which are abundant in both temperate and tropical nearshore habitats (Compagno 1984). Off Japan, one of the most common species is *Mustelus manazo*, which is distributed in the western North Pacific from Hokkaido, Japan south to the western Indian Ocean. They are born at about 30 cm total length, TL, and reach a maximum TL of about 117 cm (Compagno 1984).

Two studies on the age and growth of *Mustelus manazo* off Japan produced theoretical growth curves which suggested that the southern populations, near Nagasaki (Tanaka and Mizue 1979), grow faster but do not reach as large an asymptotic length as those in the waters off northern

Japan, near Choshi (Taniuchi et al. 1983). Both of these studies used growth bands from vertebral centra as interpreted from the sectioned and haematoxylin-stained sections of 400 and 256 specimens, respectively.

Growth in elasmobranch fishes has often been described by the von Bertalanffy growth equation using a variety of techniques to fit a curve to the observed data (see Cailliet et al. 1983a; Cailliet et al. 1986a,b for reviews). However, the curves that result from such mathematically derived parameters often hide important details on the real variance in the data.

Several sources of this variance can be identified. One is preparation technique. Elasmobranch vertebral centra can be studied whole, sectioned, stained, cleared with various chemicals, x-rayed, or by using a combination of these procedures (Cailliet et al. 1983a). Another source of variance is reader accuracy and precision. If only one reader inteprets the number of bands in the calcified structure being used, personal variation may arise in repeated counts of the structure and can make assigning a band number difficult. In other cases, inter-reader differences in band counts could result from variation in band interpretation. Sample size and sample biases are a third source of variation. Often, the largest and/or the smallest size classes are unavailable, one sex is more abundant in the study site, or seasonal variation in the collection of specimens biases the fit of the model to the data.

A fourth source is individual fish variation. Models tend to produce simple curves which are presumed to adequately represent the ''typical'' growth of a species. However, individuals vary a great deal, presumably as a result of genetic growth abilities, type and abundance of food, energy conversion efficiencies, and environmental factors. Thus, the lack of fit of a growth model might be explained by this individual variation.

Before we can definitely state that the two populations of *Mustelus manazo* have different growth characteristics (Taniuchi et al. 1983; Tanaka 1984), these possible sources of variation need to be investigated. One way to approach this question is to assess the precision and error inherent in multiple readings of the calcified structures used in age analysis (Beamish and Fournier 1981; Chang 1982). The original papers used data derived from counts by individual readers within one institution, and no assessment of variation was attempted.

Most authors have assumed that there will be variation in size at estimated age and that this could be expressed by vertical error bars in a growth curve (Fig. 1a). However, few authors have considered the impact on a growth curve of high error and low precision associated with counts and interpretations of growth zones in calcified structures. For example, for a fish age 3, a 6% error would result in a difference of 0.18 years in the age at size determined by age analysis (Fig. 1b). In addition, this error is age-specific. For example, if the age was estimated to be higher, say 10 years, and there was a 20% error, this could cause the age estimate to be off by 2 years (Fig. 1c). Whereas, at age 3, a 20% error could result in a discrepancy of 0.6 years, which is 20% of the actual age estimate (Fig. 1d). Thus, it is important that both types of error be considered when comparing growth curves.

Another potential source of error, which could seriously influence statements that growth characteristics differed between species, populations, or sexes, is how well the model being employed to characterize growth fits the data. For example, in a study of the age and growth of three pelagic shark species off California, Cailliet et al. (1983b) concluded that the von Bertalanffy growth model adequately characterized the growth of *Alopias vulpinus* and *Prionace glauca*, but not *Isurus oxyrinchus*. This disparity was most likely due to small and biased samples of the last species, but it could very well be that *I. oxyrinchus* populations do not grow according to this growth model.

The purpose of this study was to evaluate these sources of variation relative to the perceived differences in growth between the two populations of *Mustelus manazo*. The approach involved a cross-population, cross-reader comparison, between U.S. and Japanese collaborators, of the band counts from centrum sections.

In addition, vertebral centra of *M. californicus* and *M. henlei* that had been previously used for an age and growth study using X-radiography (Yudin 1987; Yudin and Cailliet 1990), were sent to Japan for haematoxylin staining to compare band counts between the U.S. and Japanese collaborators using the two methods. Finally, a comparison was made among growth parameters estimated for other species of *Mustelus* (Francis 1981; Yudin 1987; Yudin and Cailliet 1990) using other techniques.

Materials and Methods

Thirty sectioned vertebral centra of *Mustelus manazo* from both sexes and locations were selected from samples that were used in the two original studies (Tanaka and Mizue 1979; Taniuchi et al. 1983), resulting in a total of 120 sections. The size range from which sections were taken was similar for both populations, with total lengths ranging from 680 to 800 mm (Fig. 2). However, there were fewer of the larger (>740 mm TL) specimens available from the Nagasaki sample. The overall size ranges were similar to those reported in the original studies, but were somewhat narrower than the 300–1100 mm overall size range reported for the species by Compagno (1984). Band counts on the 120 sections were compared within and between laboratories. Details of the preparation, sectioning, and haemotoxylin staining methods are available in the original papers.

The 60 samples from each of the two populations were read by S. Tanaka at Tokai University, Japan, and by

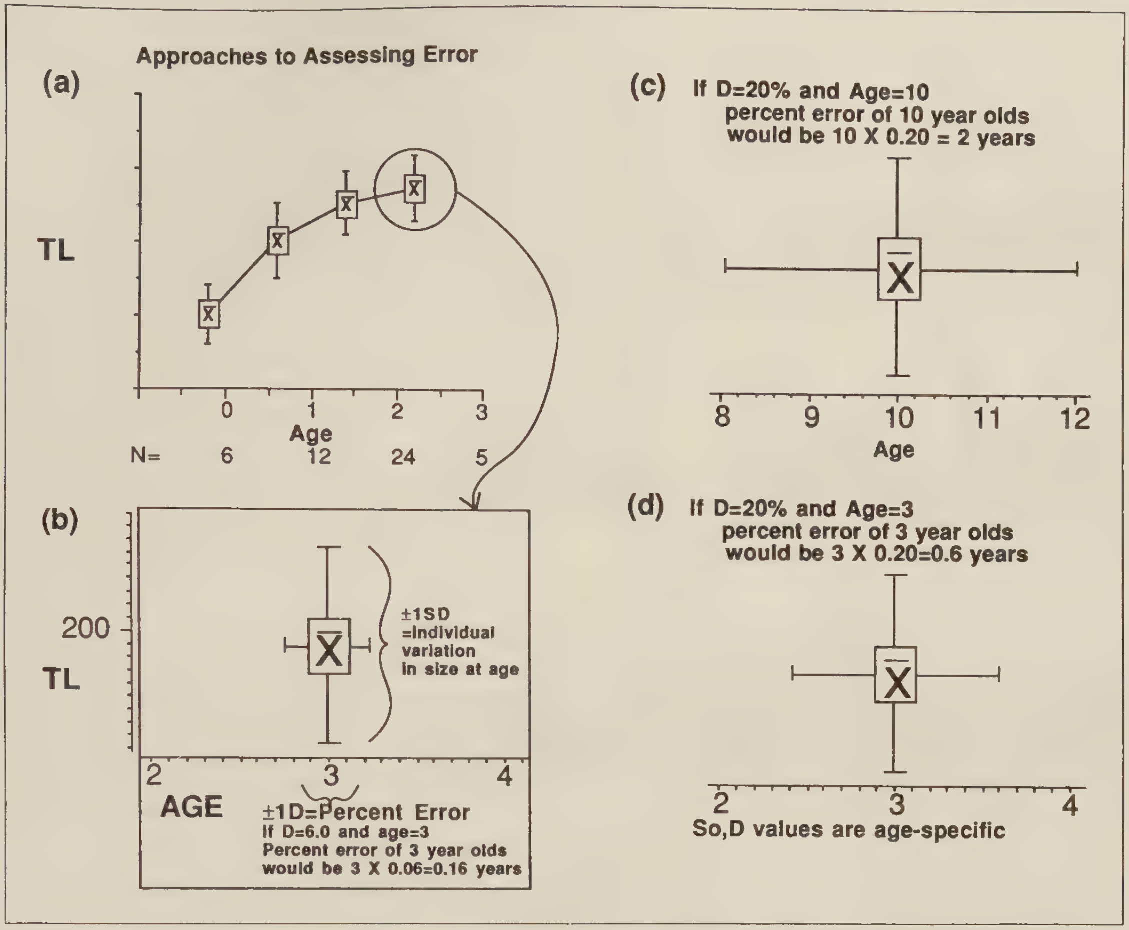
(a)
Approaches to Assessing Error
TL
0
1
2
3
Age
N= 6 12 24 5
(b)
200
TL
±1SD =individual variation in size at age
2
3
4
AGE
±1D=Percent Error
If D=6.0 and age=3
Percent error of 3 year olds would be 3 X 0.06=0.16 years
(c) If D=20% and Age=10
percent error of 10 year olds would be 10 X 0.20 = 2 years
8 9 10 11 12
Age
(d) If D=20% and Age=3
percent error of 3 year olds would be 3 X 0.20=0.6 years
2 3 4
So,D values are age-specific

Figure 1.
Diagram demonstrating how variation in the sizes at age and percent error of age estimates can influence growth curves of fishes: (a) a typical growth curve showing mean total lengths (TL) and their standard deviations (SD) at each age; (b) the influence at age 3 of individual variation in size at age (vertical bars = 1 SD) and a 6% error (D) of the age estimate; (c) the influence at age 10 of a 20% error on the age estimate; and (d) the influence at age 3 of a 20% error on the age estimate.

G. Cailliet and K. Yudin at Moss Landing Marine Laboratories (MLML). Precision of age determinations was assessed within MLML counts, and between Japanese counts and a consensus was reached by MLML readers. A consensus was reached when at least two of three readings were identical, or in rare cases by using the median of three counts.

Three measures of precision were calculated. The first was average percent error (A.P.E.), which measures the average deviation of readings from the means of all readings of each section (Beamish and Fournier 1981). The second was percent error (D), an alternate index of precision proposed by Chang (1982), which is calculated by dividing the coefficient of variation (V) of readings by the square root of the number of times each fish is aged (R), then multiplying this figure by 100. Chang (1982) felt this was a better precision estimator because it is unbiased and consistent over all samples. The third was to calculate the percentage of the readings that agreed by ±1, 2, 3, etc. bands among all counts for the particular sample in question. These were also presented graphically as a histogram of the percent agreement. For each sex and location, the number of centra available for analysis (n) was 30, but the number of counts (N) used in the precision analysis was not always the same. In most cases, when the counts of three readers were compared, N would be 90. In a few cases, when there were some unreadable centra, the n or N was not exactly 30, and therefore N was not exactly 90.

Age estimates taken from the original Japanese band counts were then plotted against total length and presented as means and 95% confidence intervals. Growth was plotted separately for both sexes and locations. Thus, potential sexual differences in growth would not interfere with the ability to distinguish inter-populational differences. The range of percent error (D) values calculated from

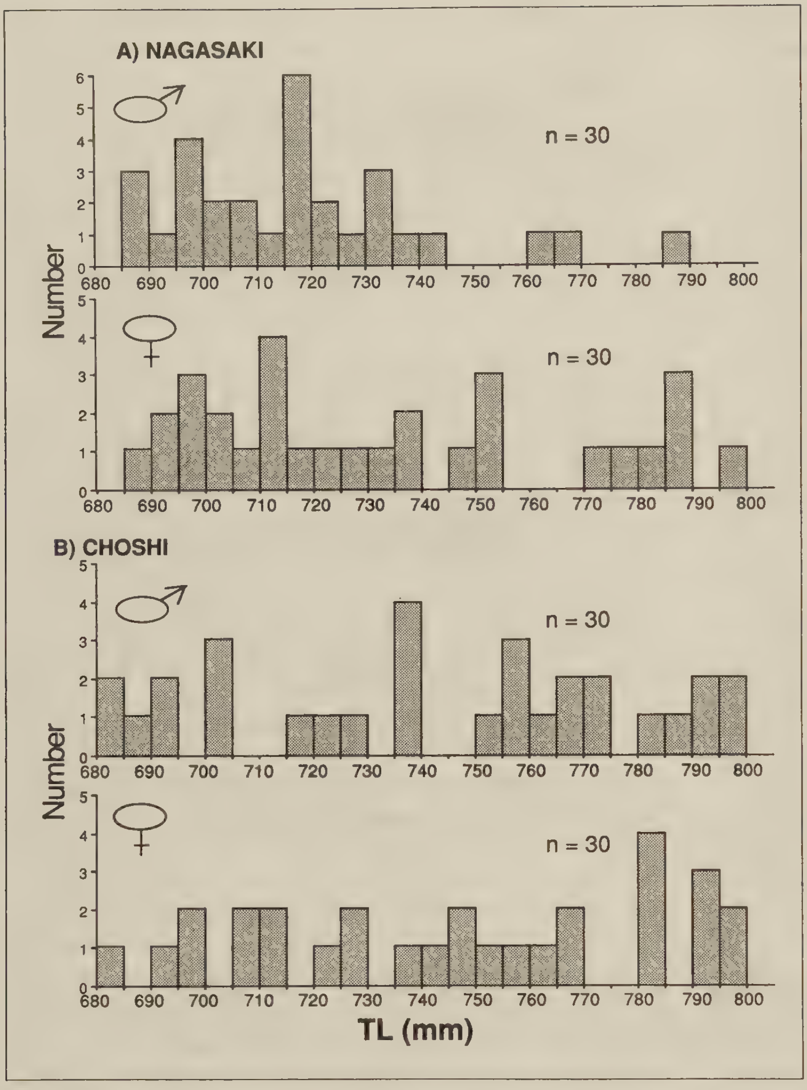

Figure 2.
Size-frequency histograms showing the samples used in the comparative age analysis of male and female *Mustelus manazo* from Nagasaki and Choshi.

inter-reader comparisons was noted on these growth curves so that potential error, in estimated years, could be assessed.

The von Bertalanffy growth function (VBGF) was fitted to all of the original Japanese size and age estimate data using a program for IBM personal computers called FISHPARM (Prager et al. 1987). This program implements Marquardt's (1963) algorithm for nonlinear least squares parameter estimation, which allows the parameters of the equation to be estimated without transforming the data into a linear form. It also minimizes the sum of squared errors through an iterative procedure and allows standard errors and 95% confidence intervals to be calculated for each of the three VBGF parameters (L_∞, K, and t_0).

The precision estimates, growth plots, and VBGF parameters were then used to evaluate whether the previously perceived differences in growth rates of the two populations of *Mustelus manazo* were real.

Vertebral centra from the two California species (*Mustelus henlei* and *M. californicus*) were sent to S. Tanaka at Tokai University for sectioning and staining with haematoxylin and band counting, to see if preparation technique or reader variability might influence the age estimates. In addition, stained and x-rayed centra from the same individuals of these two species were directly compared to see if the bands that were darkly stained with haematoxylin corresponded to the more highly calcified (opaque) or less highly calcified (translucent) bands in x-rays.

Results

Precision of band counts was relatively high for the Nagasaki sections of 4–6 year old sharks (Fig. 3). Counts made within MLML had percent errors (D) of 8.9% and 8.6% for males and females, respectively. In addition, the counts were within ±2 bands more than 93% of the

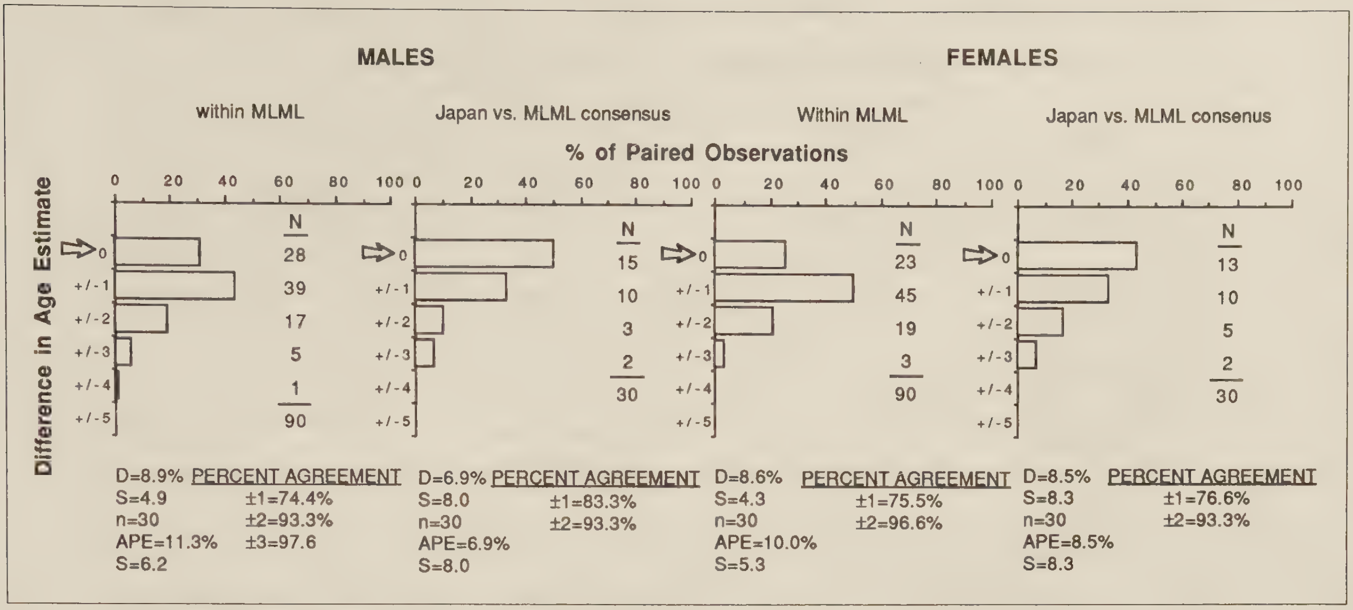

Figure 3.

Precision of age determination of male and female *Mustelus manazo* from Nagasaki. Histograms represent the difference (as the percentage of paired band counts differing by 0, 1, 2, etc. years) between readers within MLML and between Japan and MLML readers. The proportions of counts which agreed within a certain number of band counts are listed under "percent agreement," while D, S, and APE represent Beamish and Fournier (1981) and Chang's (1982) "percent error," its standard deviation, and "average percent error," respectively. The letter *n* represents the number of samples (centra) aged during this study, while *N* is the number of comparative readings of those centra.

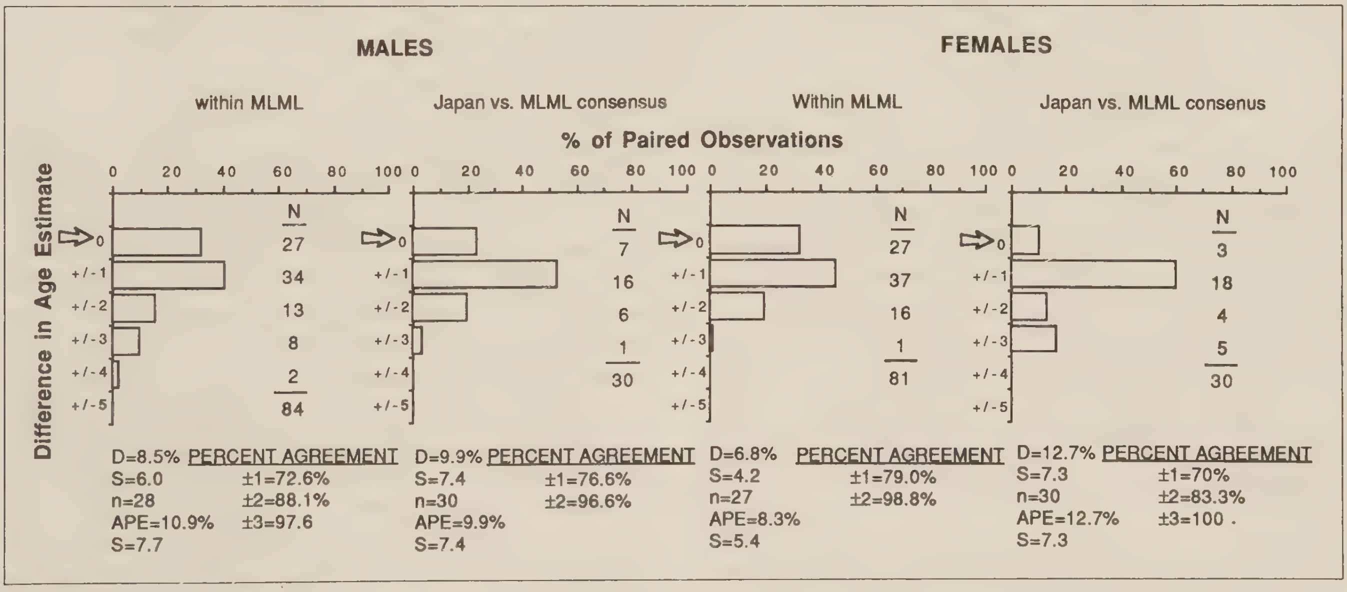

Figure 4.

Precision of age determination of male and female *Mustelus manazo* from Choshi. Details as explained in Figure 3.

time. The Japanese versus MLML counts also had relatively good precision, with D values of 6.9% and 8.3% for males and females, respectively, and more than 93% of the counts agreed within ± 2 bands.

Similarly, the Choshi samples had consistent precision age estimates (Fig. 4). Counts by MLML readers had relatively low percent errors, with D values of 8.5% and 6.8% for males and females, respectively. However, only

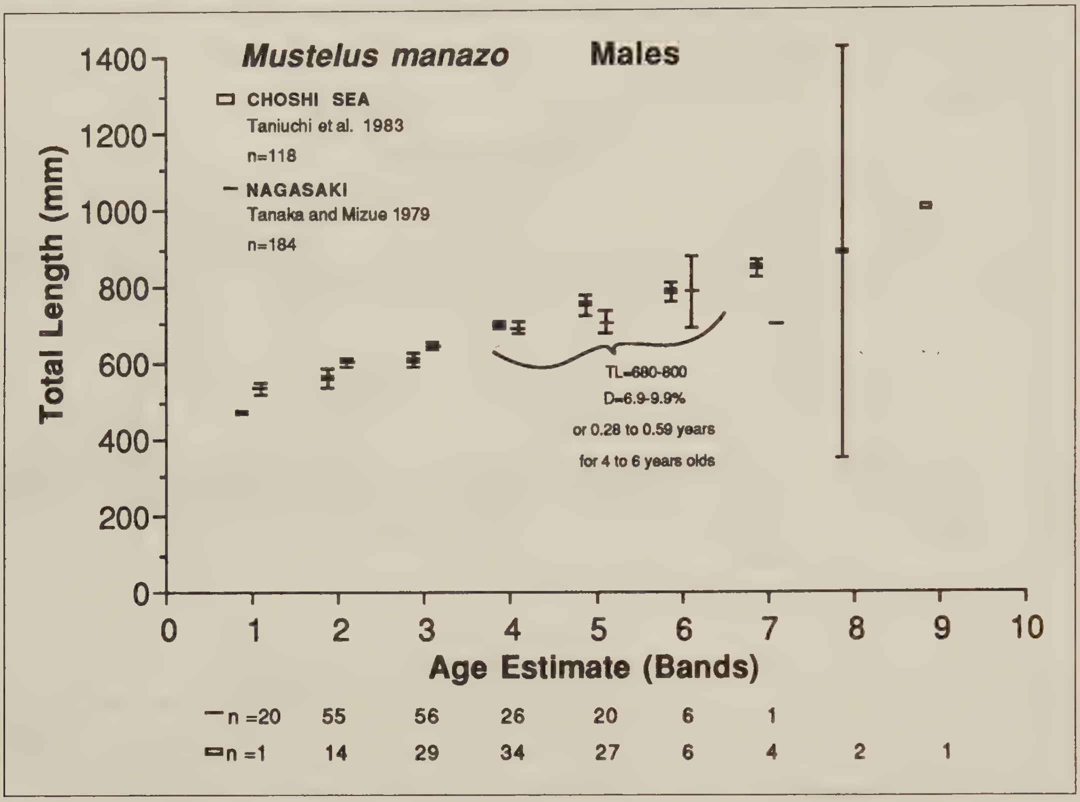

Figure 5.

Growth plots for male *Mustelus manazo* from Choshi (open box) and Nagasaki (closed line) expressed as mean size at age estimate (band counts), with vertical bars representing 95% confidence intervals of the mean, and *n* being the sample size at each age for each location. At TLs between 680 and 800 mm, age estimates ranged between 4 and 6 years, and percent errors (D) are presented from this study.

88.1% of the counts were within ± 2 bands for males, while 98.8% of females were within ± 2 bands. The Japanese versus MLML counts were less precise, with D values of 9.9% and 12.7% for males and females, respectively. In this case, 96.6% of the male counts agreed within ± 2 bands, but only 83.3% of the female counts had that level of agreement.

The growth plots for males did not appear to be different between the Nagasaki (n = 184) and Choshi (n = 118) samples (Fig. 5). Mean total lengths and 95% confidence intervals for the two populations overlapped in all but the first age classes. Very broad confidence intervals were evident for two ages (6 and 8), primarily owing to low sample sizes. Percent errors (D) ranged from 6.9 to 9.9, which, in sharks estimated at 4 to 6 years old, translates to an error of between 0.28 to 0.59 years.

The growth plots for the 216 Nagasaki and 138 Choshi females likewise did not appear to be different between the two populations (Fig. 6). Mean total lengths and 95% confidence intervals overlapped at most ages, with nonoverlapping occurring only at ages 2, 3, and 5. Broad confidence intervals only occurred at age 9, where the sample size was very small. The range of percent error values from 8.5 to 12.7% superimposed on the plot for females translates to an error of between 0.34 and 0.76 years.

The VBGF parameters calculated in this study using the original Japanese count data were somewhat different from those originally published (Table 1), probably owing to the use of FISHPARM. They still suggest, however, that *Mustelus manazo* from Choshi grow slower but reach a larger asymptotic length than those from Nagasaki. Growth coefficients (K) for both males and females from Nagasaki were higher (0.22 and 0.20) than those from Choshi (0.10 and 0.07) and their confidence intervals were narrow. The asymptotic length of males from Choshi (L_∞ = 1334 mm) appeared to be considerably higher than that from Nagasaki (L_∞ = 846 mm), but their confidence intervals overlapped, indicating that they were not different. Likewise, Choshi females (L_∞ = 1765 mm) appeared to get larger than Nagasaki females (L_∞ = 998.7 mm) but their confidence intervals also overlapped.

Tanaka's band counts on vertebral centra of the two California species of *Mustelus* that were sectioned and stained with haematoxylin were virtually identical to those obtained by Yudin (1987) and Yudin and Cailliet (1990) on centra from the same individuals that had been x-rayed.

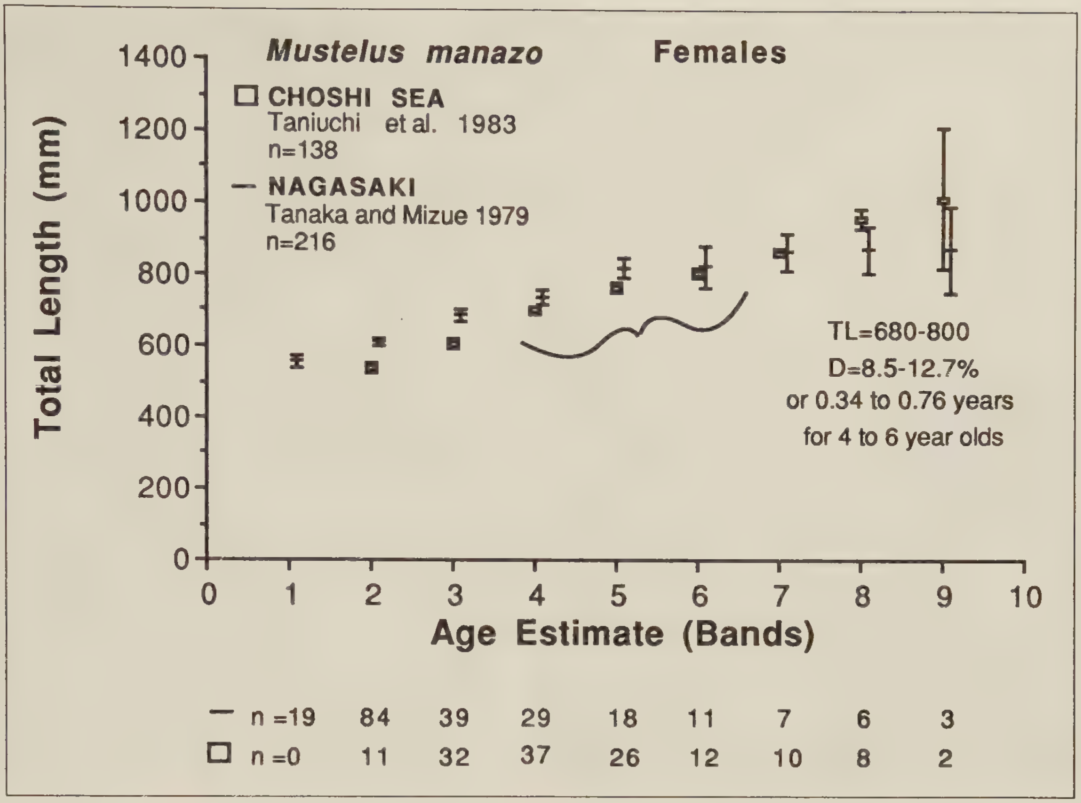

Figure 6.
Growth plots for female *Mustelus manazo* from Choshi and Nagasaki. Details as explained in Figure 5.

Table 1.
Comparative von Bertalanffy growth parameters among three *Mustelus* species from Japan and California. The Choshi and Nagasaki parameters in parentheses were those originally published, while those without parentheses were calculated in this study from the same data (Tanaka and Mizue 1979; Taniuchi et al. 1983). The parameters for *Mustelus henlei* and *M. californicus* are from Yudin (1987) and Yudin and Cailliet (1990). 95% confidence intervals (C.I.) are given to the immediate right of each VBGF growth parameter.

	Von Bertalanffy growth parameters						
	L_∞	C.I.	K	C.I.	t_0	C.I.	n
Mustelus manazo							
Choshi							
Males	1334	472.4	0.10	0.01	– 3.42	1.72	118
	(1043)	—	(0.19)	—	(– 2.00)	—	″
Females	1765	709.6	0.07	0.04	– 3.29	1.33	138
	(2771)	—	(0.03)	—	(– 4.77)	—	″
Nagasaki							
Males	846	146.9	0.22	0.02	– 3.69	2.32	184
	(714)	—	(0.70)	—	(– 0.73)	—	″
Females	999	110.7	0.20	0.01	– 2.88	1.15	216
	(886)	—	(0.38)	—	(– 1.13)	—	″
Mustelus henlei							
Males	861	195	0.28	0.20	– 1.09	0.93	15
Females	976	68	0.23	0.06	– 1.38	0.69	56
Mustelus californicus							
Males	1018	185	0.35	0.18	– 1.00	0.42	27
Females	1424	165	0.22	0.06	– 1.03	0.30	31

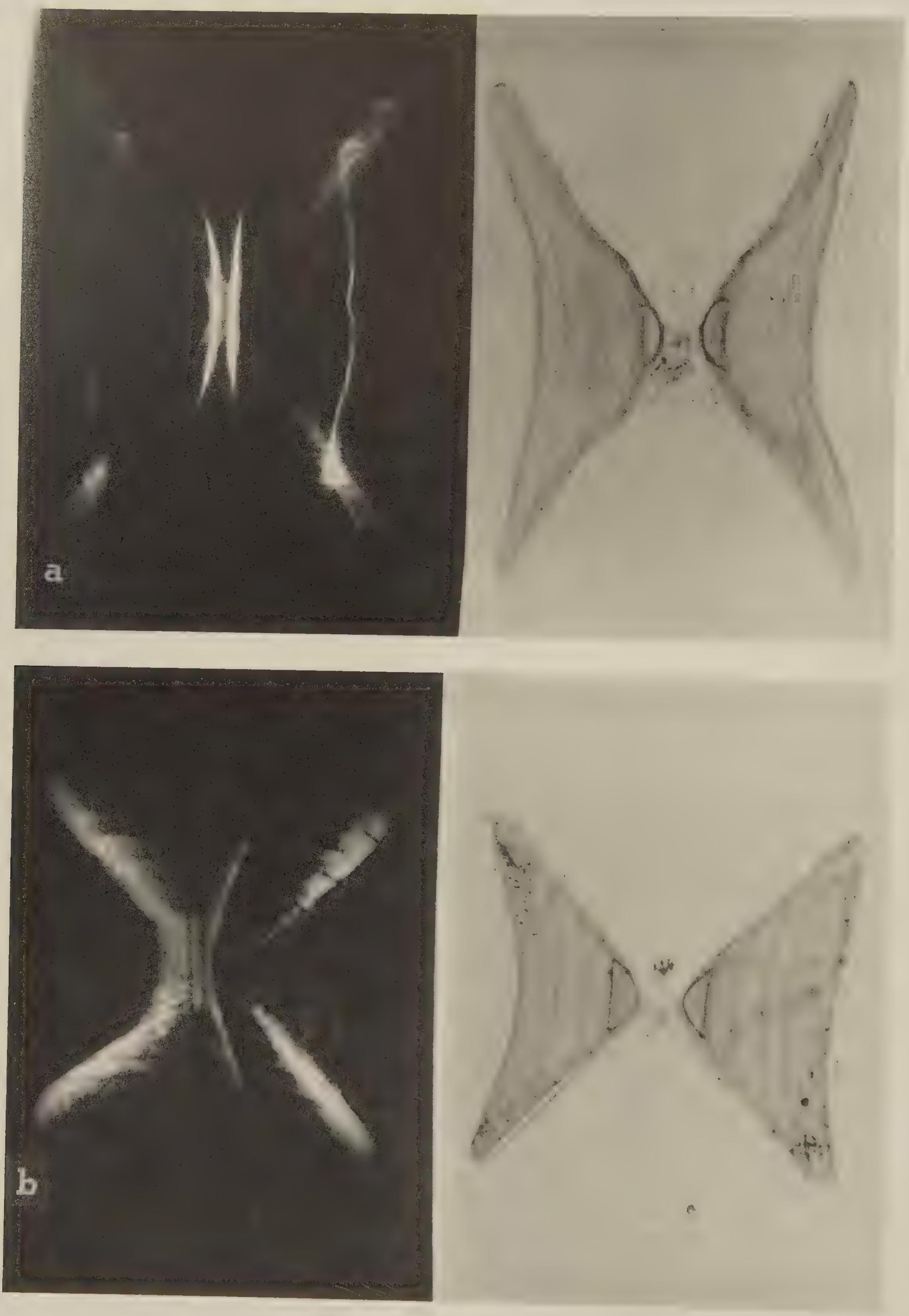

Figure 7.
Comparison of growth zones of sections of *Mustelus henlei* and *M. californicus* vertebral centra which have been (a) stained with haemotoxylin and (b) x-radiographed. Note that the dark zones in the stained section are the same as those which are calcified (white) in the x-radiographs of both species.

The darkly haematoxylin-stained bands in sections prepared by Tanaka are those bands that appear highly calcified (white) in x-radiographs by Yudin (1987) and Yudin and Cailliet (1990) (Fig. 7). Thus, these two techniques produced identical results.

The VBGF parameters for *Mustelus manazo* were comparable to those of the two California species (Table 1). The asymptotic lengths of all three species were relatively small, with the L_∞ values of 846–1765 mm TL for *Mustelus manazo* being between those of 861–976 mm TL for *Mustelus henlei* and 1018–1424 mm TL for *Mustelus californicus*. In all three species, and in those studied by Francis (1981), females appear to grow larger than males, although the difference may not be statistically significant in all cases.

Discussion

The apparent differences in VBGF growth parameters between the two Japanese populations of *Mustelus manazo* (Tanaka 1984) are not significant when reader precision, analysis of mean size at age, and goodness-of-fit are considered. For the size range studied, percent error values were relatively low, ranging from 6.9% to 12.7%, and agreements within ± 2 years occurred in over 93% of the readings (Figs. 3, 4). This translates into a potential error, for 4 to 6 year olds, of between 0.28 and 0.76 years, which would not seriously influence mean size-at-age data (Figs. 5, 6), nor the growth coefficients, asymptotic lengths, or longevity estimates.

However, the poor goodness-of-fit of the VBGF to the data was probably the major problem in interpreting the characteristic growth of the two populations of this species. The confidence intervals calculated indicate that the L_∞ values are not very good estimates (Table 1). In addition, a critical look at the shape of the empirical plots in Figures 5 and 6 would suggest that these are not shaped like the typical von Bertalanffy growth curves, but rather are linear. Further, the influence of several of the data points for older individuals, which suffer from small sample size as well, results in high estimates of the asymptotes and their respective confidence intervals, especially for Choshi sharks (Figs. 5, 6; Table 1). Thus, the VBGF might not be the appropriate model to use for the growth of this species; it certainly provides variable and often misleading parameters.

When studying possible inter-population or inter-specific differences in growth, several additional considerations are necessary. First, one must consider sample sizes and biases. In this case, the sample sizes were quite large and the biases were unavoidable in that there were (as is typical) too few very small and very large individuals.

Second, the same or equivalent techniques of preparation and readings should be used. In this case, all samples were sectioned and stained with haematoxylin, and these inter-technique comparisons produced comparable results.

Third, reader accuracy and precision must be considered. In this case, owing to the relatively short longevity of this species and the good readability of growth zones, precision was acceptable.

Fourth, individual variation should be taken into consideration. Empirical size-at-age data, such as those presented in Figures 5 and 6, allow for individual variation to be expressed, while curve fitting does not.

Fifth, if one is going to use a growth model, such as the VBGF, the goodness-of-fit must be considered. The linear fits initially used (Tanaka and Mizue 1979; Taniuchi et al. 1983; Tanaka 1984) produced very different VBGF parameters from the nonlinear, curve-fitting program (FISHPARM; Prager et al. 1987) used in this study. In addition, standard errors and confidence intervals can be calculated using these nonlinear techniques, and these provide sufficient statistical information to place a certain confidence around the growth parameters produced. If the confidence interval is high, then the goodness-of-fit would be low, and the model is probably inappropriate.

Finally, some verification of the temporal periodicity with which the growth bands are deposited is essential if one is to accurately assess the meaning of the band counts (Cailliet et al. 1986b). The ideal approach is to have known growth and band deposition, which is possible with tetracycline marking and tag-recapture growth estimates, as was accomplished by Smith (1984) for *Triakis semifasciata*.

This study provides ample evidence that inter-population comparisons of the Japanese smoothhound, *Mustelus manazo*, cannot legitimately be made without considering all of the above factors. Indeed, the major reason for the false perception that these two populations had different growth rates was an acceptance of VBGF parameters, without a critical look at the actual data. This should be avoided at all costs in future studies on the growth of fishes.

Acknowledgments

We thank the numerous students at Moss Landing Marine Laboratories who have been involved in elasmobranch age and growth studies. We are especially indebted to Jim Brennan for his aid in counting growth bands and photographic sections. Lynn McMasters did the illustrations. The United States–Japan Cooperative Research Project, funded by the National Science Foundation and the Japanese Society for the Promotion of Science, made the travel for this project possible. The research was sponsored in part by NOAA, National Sea Grant College Program, Department of Commerce, under grant numbers 04-8-M01-189 and NA80AA-D-00120; by the California Sea Grant College Program under project numbers R/F-81 and A/S-2; and in part by the California State Resources Agency. The U.S. Government is authorized to reproduce this paper and distribute it for governmental purposes.

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Differences in Growth of the Blue Shark, *Prionace glauca*: Technique or Population?

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ABSTRACT

We have used a cross-exchange, dual method, and comparative reading approach to determine if apparent differences in growth curves and von Bertalanffy growth parameters from two areas in the Pacific are due to population (i.e., genetic and/or environmental) characteristics, methodologies, sampling, or the statistics used to characterize growth. Vertebrae were collected from blue sharks, *Prionace glauca*, off California and Japan in previous studies (Cailliet et al. 1983b; Tanaka 1984). Two techniques, silver nitrate staining and sectioning of vertebral centra, were used in age determination. Results varied considerably among readers and shark sizes. Some of the differences in growth between populations could have been due to the methodology used, the interpretation of growth zones, and the goodness-of-fit of von Bertalanffy growth function (VBGF) to the data. Population and environmental effects cannot be confidently used to account for the suggested differences in growth curves among these populations of blue sharks. Real differences, if they exist, are obscured by variability due to methods, interpretation, and statistical fit.

Introduction

The blue shark, *Prionace glauca*, is a cosmopolitan pelagic, wide-ranging carcharhinid which occurs in temperate and tropical waters, with peak abundances between lat. 20° and 50°N (Compagno 1984). It is reported to have notable seasonal movement patterns, with abundances increasing in high latitudes in the summer and in low latitudes in the winter (Suda 1953; Strasburg 1958; Compagno 1984; Nakano et al. 1985).

Owing to its abundance, relatively accessible epipelagic habits, and fishery potential (Colvocoresses and Musick 1980; Cailliet and Bedford 1983; Tanaka 1984; Anderson et al. 1985; Holts 1988), the life history of the blue shark has been the subject of many studies (reviewed by Compagno 1984). The age and growth of blue sharks have been studied in three geographically distinct regions, the North Atlantic (Stevens 1975; Skomal et al. 1988; Skomal 1989), the northeast Pacific (Cailliet et al. 1983b), and the northwest Pacific (Tanaka 1984). Aasen's (1966) length-at-age data derived from length frequencies were fit to the von Bertalanffy growth function (VBGF) by Stevens (1975), but the specific sampling location in the North Atlantic was not reported.

Results of these papers on age and growth of blue sharks suggest that VBGF parameters differ among locations (Table 1). This implies that the growth characteristics of each population are influenced by different genetic and/or environmental parameters. However, growth that is described using the VBGF can often overlook important details which result from variance in the data. Sources of this variance include preparation technique, reader accuracy and precision, sample size, sample biases, and individual variation in size at age (see Cailliet et al. 1990, for additional discussion). These sources of variance can cause a serious problem when fitting a growth model that might not accurately characterize the growth of a species.

Table 1.
Von Bertalanffy growth parameters from five samples of *Prionace glauca* from four different locations. Numbers in parentheses for Skomal's (1989) data are standard errors, while those for Tanaka's (1988) data represent 95% confidence intervals calculated using FISHPARM (Prager et al. 1987). F, M, and B refer to females, males, and both sexes combined. Total lengths are expressed in cm. The VBGF model was fit to Aasen's (1966) length-at-age and size frequency data by Stevens (1975). The VBGF parameters from Skomal (1989) were converted from fork length to total length, according to conversions in Pratt (1979), and those preceded by an * were calculated from length/frequency analysis.

Authors	Location	Sex	L_∞	K	t_0	n
Aasen 1966	N. Atlantic	*B	394	0.13	-0.80	268
Stevens 1975	N.E. Atlantic	B	423	0.11	-1.04	82
Cailliet et al. 1983b	N.E. Pacific	F	242	0.25	-0.80	88
		M	295	0.18	-1.13	38
Skomal 1989	N. Atlantic	F	375 (6.9)	0.15 (0.008)	-0.87 (0.10)	93
		*F	350	0.10	-1.47	2515
		M	343 (1.0)	0.16 (0.002)	-0.89 (0.03)	212
		*M	375	0.16	-0.86	4029
Tanaka's 1984 data (this study)	N.W. Pacific	F	304 (62.2)	0.16 (0.07)	-1.01 (0.61)	152
		M	369 (137.1)	0.10 (0.07)	-1.38 (0.93)	43

To determine whether different populations of blue sharks have different growth characteristics (Tanaka 1984), these sources of variation need to be investigated. One way to approach this question is to assess precision and error in multiple readings of the calcified structures used in age analysis (Beamish and Fournier 1981; Chang 1982). The potential for lack of precision or high error to confound a growth curve is explained in detail by Cailliet et al. (1990).

To further investigate the differences in VBGF parameters for blue sharks from two of the four geographic regions, we used a cross-exchange, dual method, and comparative reading approach to assess whether sampling, sample preparation methodologies, reader precision and error, and/or model fitting might cause problems that would prevent inter-population comparisons from being significant.

Materials and Methods

For the comparative ageing part of this study, we used vertebral centra from female blue sharks taken in the western Pacific off Japan (Tanaka 1984) and in the eastern Pacific off California (Cailliet and Bedford 1983; Cailliet et al. 1983b). We chose samples from 20 "small" (<155 cm TL) and 20 "medium" (155–215 cm TL) blue sharks from Japan and from 15 "medium" and 15 "large" (>215 cm TL) blue sharks from California waters. Centra from both locations were sectioned and stained with haematoxylin by the senior author at Tokai University, and were prepared whole at Moss Landing Marine Laboratories (MLML), using a modified silver nitrate staining technique (Cailliet et al. 1983a,b).

The stained sections and centra were exchanged between the Japan and California laboratories and readings were compared. Whole centra were read only by MLML personnel, since the stained bands did not last over time very well. The stained sections were read by both Japanese (Tanaka) and MLML (Cailliet and Yudin) readers. In some cases, there was sufficient variation among readings of the same centrum that a consensus, defined as two or more readings that were identical, had to be reached. Centra were classified as unreadable if a consensus could not be reached.

The precision of age determinations was assessed for each of the three size classes (small and medium from Japan; medium and large from California) within locations and techniques, and between locations and techniques using average percent error (Beamish and Fournier 1981), percent error (Chang 1982), and percent agreement (see Cailliet et al. 1990, for details on the equations involved, and Table 2 for an outline of comparisons made). These techniques allowed us to evaluate errors in age estimation, which should prove useful in comparing growth curves between species or populations which used different readers and techniques.

Age estimates (both sexes combined) from the original Japanese blue shark counts by Tanaka (1984, pers. data) and the California blue shark counts by Cailliet et al.

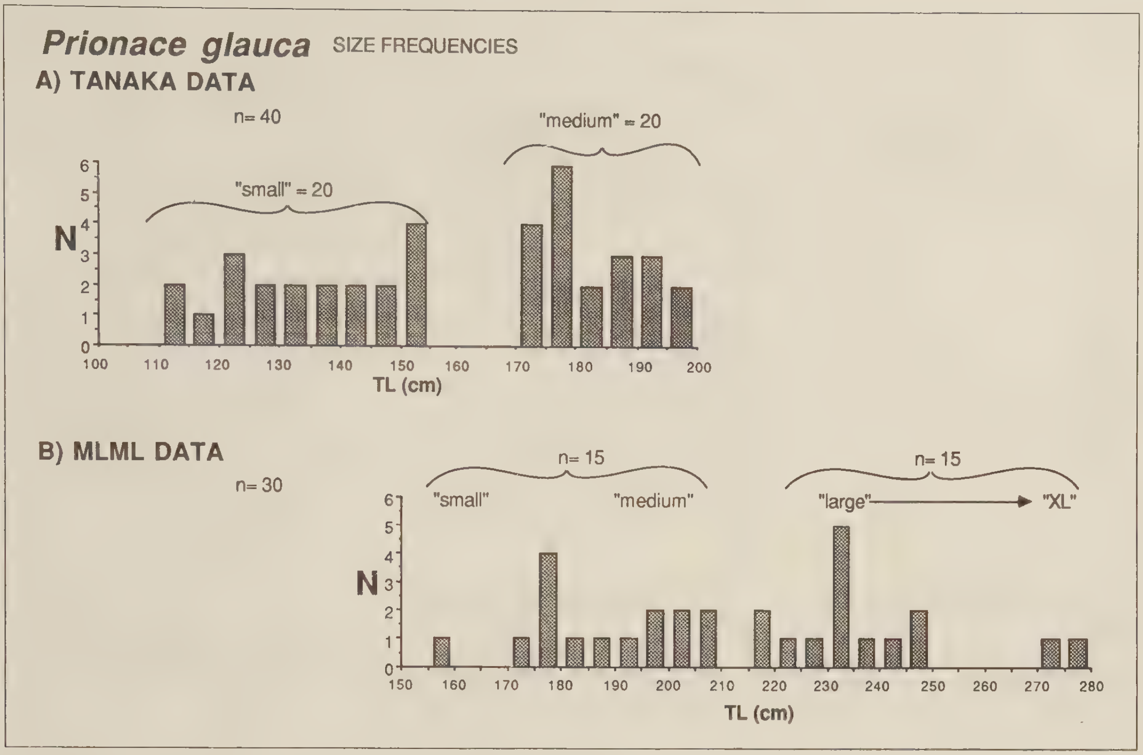

Figure 1.
Size-frequency histograms of the samples used in the comparative age analysis of female *Prionace glauca* from Japan (Tanaka data for small and medium sharks), and from California (MLML data for medium and large sharks). Total lengths (TL) are in cm.

(1983b) were plotted against total length, presented as means and 95% confidence intervals on the same graph, and compared. The range of percent error (D) values calculated from inter-reader and inter-technique comparisons were noted for the three size classes on these growth curves so that potential error, in estimated years, could be assessed.

Male and female data from Japan were separated and size-at-age data, also presented as means and confidence intervals, were plotted. Separate data for males and females were unavailable for the California population. The same range of percent error values were plotted for the three size classes on this curve.

The von Bertalanffy growth function (VBGF) was fitted to the original Japanese size and age estimates using a program for IBM personal computers called FISHPARM (Prager et al. 1987). This program implements Marquardt's algorithm for nonlinear least squares parameter estimation (see Cailliet et al. 1990, for further discussion of this technique). This kind of reanalysis was not undertaken for the data sets of Aasen (1966), Stevens (1975), or Cailliet et al. (1983b), primarily because of small, biased samples and lack of precision estimates. Skomal (1989) calculated standard errors around his VBGF parameters. The precision estimates, growth plots, and VBGF parameters were then used to evaluate whether or not obvious observable differences in growth rates of the two populations of *Prionace glauca* could be detected.

The size range of blue sharks from which sections were taken was different for both locations, with total lengths ranging from 110 to 200 cm TL (small and medium) for the Japanese sample, and from 156 to 280 cm TL (medium and large) for the California sample (Fig. 1). In the California sample, very large (>250 cm TL) individuals were rare. The overall size range of our sample is much narrower than that presented for blue sharks (Compagno 1984), which is between 35 and 44 cm at birth and 383 cm TL, the largest individual measured. However, our sample probably represents the commonly occurring sizes of blue sharks being studied in the Pacific regions.

Results

For the Japanese samples, the precision of band counts was consistently high for whole centra analyzed by MLML personnel (Fig. 2; Table 2). Counts made within MLML had relatively low percent errors, with D being 6.1% for both small and medium sharks, and close to 100 percent agreement within ± 2 counts.

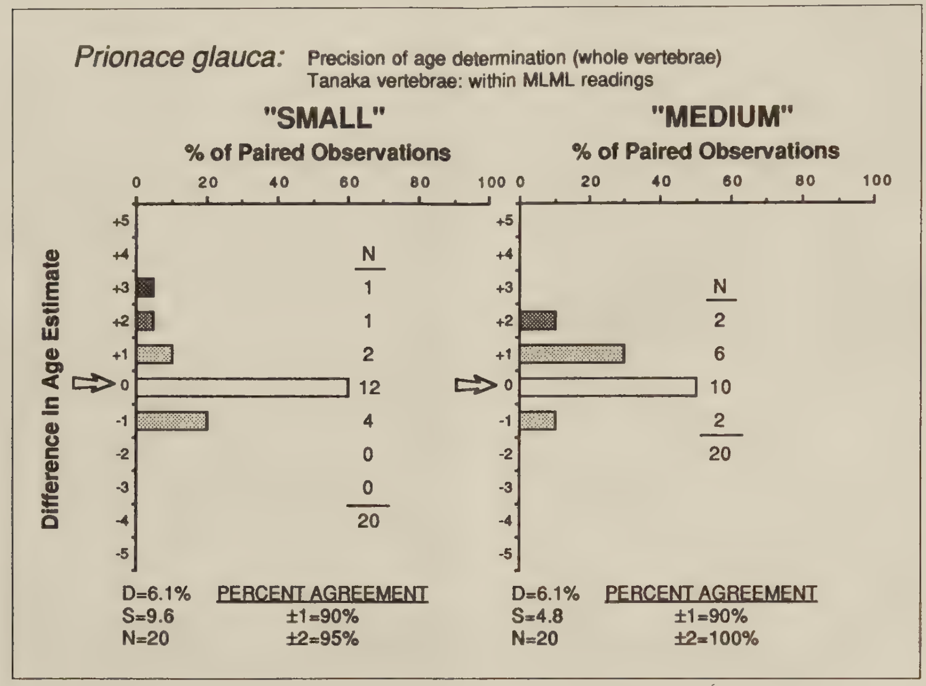

Figure 2.
Precision of age determination among MLML readers of female *Prionace glauca* from Japan (Tanaka whole vertebrae). Histograms represent the difference (as the number "N" and % of paired band counts) between readers within MLML readings. The proportions of counts which agreed within a certain number of band counts are listed under "percent agreement." The symbols D, S, and n represent Chang's (1982) "percent error," its standard deviation, and number of centra (sample size), respectively.

Table 2.
Summary of age precision analysis for *Prionace glauca* taken off Japan ("Tanaka Samples", comprising centra from 20 "small" and 20 "medium" blue sharks) and off California ("MLML Samples", comprising centra from 15 "medium" and 15 "large" blue sharks). Within each of these sample locations, percent errors (D) were calculated for age estimates of various combinations of whole and sectioned vertebral centra. Ages were determined by one Japanese (Tanaka) and two MLML (Cailliet, Yudin) readers, who are listed in parentheses. Size designations and the term "consensus" are defined in the text. No inter-reader comparisons were made of whole MLML samples.

	Sizes		
Blue shark centra	Small	Medium	Large
Tanaka samples			
Whole centra only (MLML readers)	6.1%	6.1%	—
Sectioned centra only			
(Japanese vs. MLML readers)	14.4%	24.5%	—
(MLML readers)	17.2%	7.9%	—
Whole and sectioned centra			
a. Sectioned only (Japanese vs. MLML readers)	14.4%	21.9%	—
b. Whole vs. sectioned (MLML vs. consensus)	8.2%	7.9%	—
MLML samples			
Sectioned centra only (Japanese vs. MLML readers)	—	5.1%	4.0%
Whole and sectioned centra			
a. Whole vs. sectioned (MLML readers)	—	10.5%	3.9%
b. Whole vs. sectioned (MLML vs. Japanese readers)	—	6.4%	7.3%

The precision analysis was not as consistent for sectioned centra from Japan (Fig. 3, Table 2). For small specimens, counts made within MLML had a percent error value of 17.2%, and 83.3% of the readings agreed within ± 2 counts and 94.4% within ± 3 (Fig. 3a). For medium specimens, the percent error was lower (D = 7.9%) but percent agreement was the same (Fig. 3b). Comparison of Japanese and MLML readings indicated relatively poor precision. For small specimens, D was 14.4%, but 94.4% of the counts were within ± 2 counts (Fig. 3a). For medium

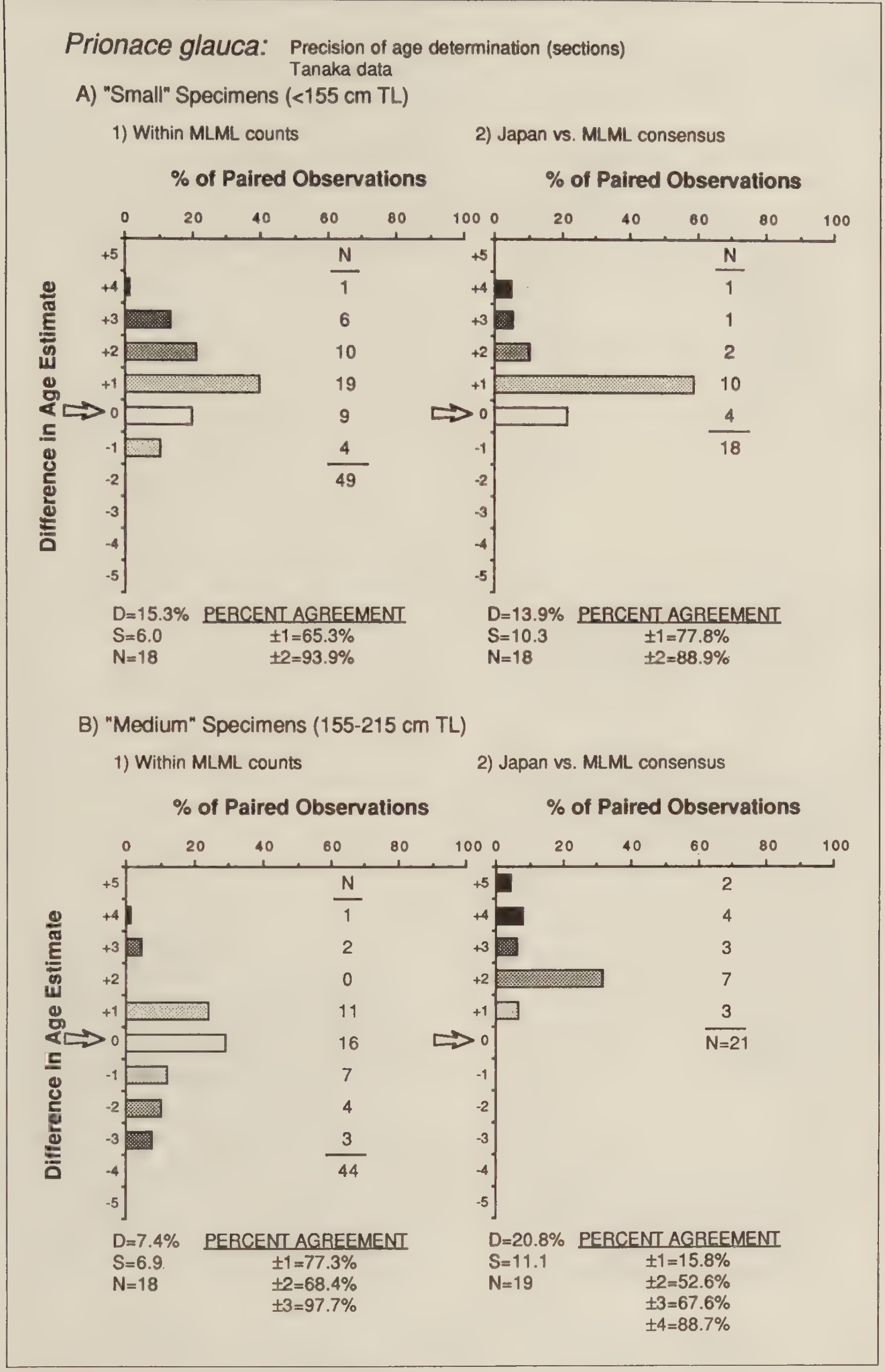

Figure 3.
Precision of age determination of female *Prionace glauca* from Japan (Tanaka sectioned vertebrae) within MLML readings and between Japanese and MLML consensus readings, for (a) small and (b) medium specimens. Details as explained for Figure 2.

specimens, percent error was quite high (D = 24.5%), and percent agreement low, with only 83.2% of the counts within ± 4 (Fig. 3b). MLML readings were consistently higher than Japanese readings of stained sections.

For the sample used to compare the sectioned vs. whole vertebrae, the precision of band counts from the Japanese blue sharks within sectioned samples of medium sizes was poorer than for small sizes, but whole vs. sectioned counts were more precise (Fig. 4; Table 2). The percent error within sectioned samples for small sharks was high (D = 14.4%) but 94.4% of the counts were within ± 2 counts (Fig. 4a). The medium shark sections were more difficult to read, with a percent error of 21.9% and only 89.5% of the counts within ± 4 counts. Whole vs. sectioned counts were more precise, with D values between 7.9 and 8.2% and with high percent agreement values (Fig. 4b).

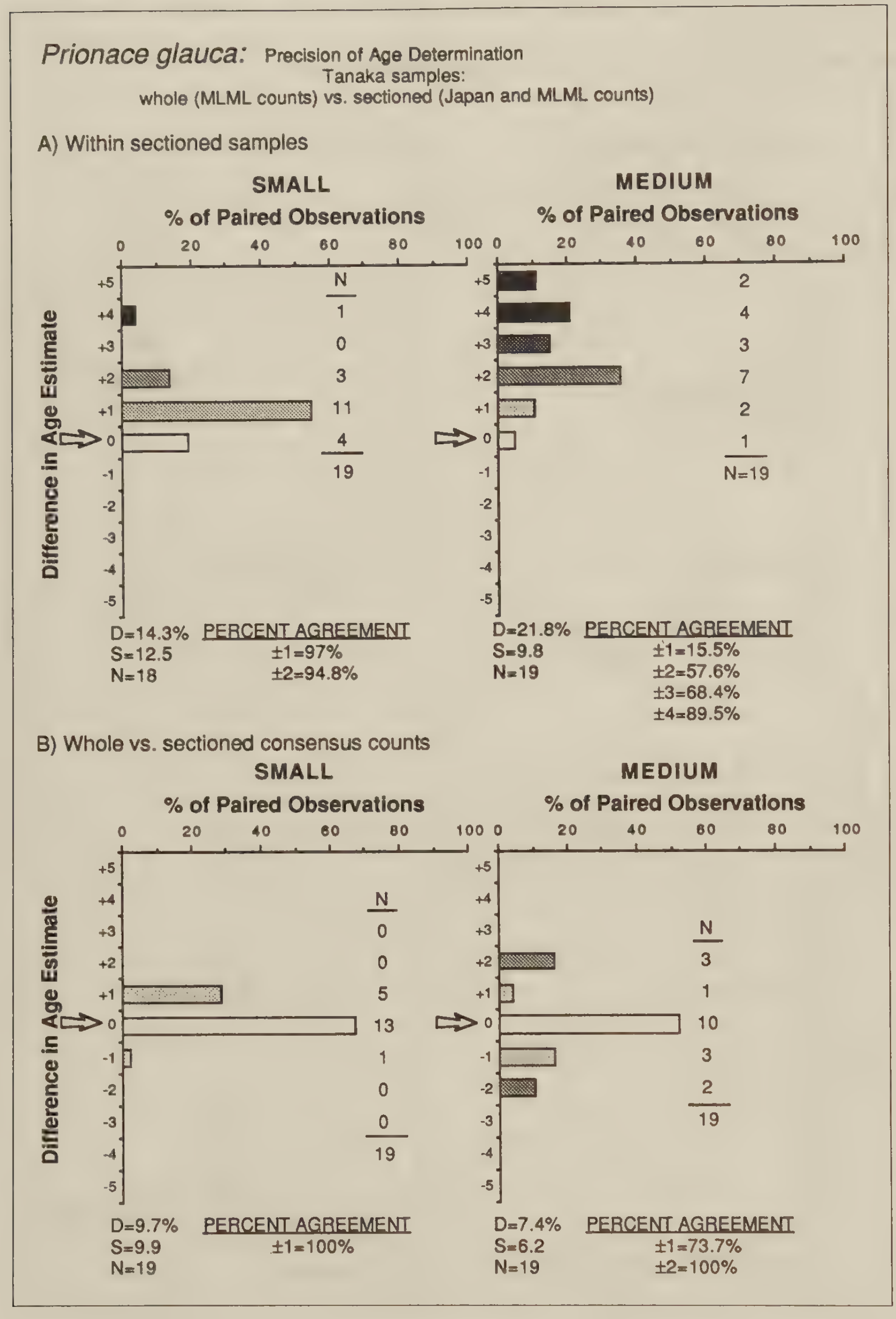

Figure 4.

Precision of age determination of female *Prionace glauca* from Japan (Tanaka whole and sectioned vertebrae). Both Japanese and MLML investigators made counts on sectioned vertebrae and the within sectioned comparisons are in (a). Only MLML investigators made counts on whole vertebrae and these are compared with a consensus of Japanese and MLML counts on sectioned vertebrae in (b). Other details as explained for Figure 2.

For the California samples, the precision within sectioned samples was less for medium shark centra than for large sharks (Fig. 5, Table 2). MLML counts on sections from medium sized sharks were consistently higher than Japanese counts, but the errors were only 5.1% and agreement was 100% within ± 2 years (Fig. 5a). For sections from large sharks, percent error was even lower (D = 4.0%) and percent agreement was 100% within ± 1 count (Fig. 5b).

Whole centra produced counts in both medium and large blue sharks which were consistently lower than sectioned centra, whether read by Japanese or MLML personnel (Fig. 5, Table 2). For medium sharks, D was 6.4% and percent agreement 93.3% within ± 2 counts for inter-technique, inter-laboratory comparisons; D was 10.5%, with only 83.3% agreement within ± 3 years using only MLML readers (Fig. 5a). Results were more variable for large sharks (Fig. 5b), with percent error values of 7.3% and 3.9% and percent agreements of 100% within ± 2 and 92.9% within ± 1 for inter-laboratory and within MLML readings, respectively. In one case, section readings produced 7 more bands than did whole vertebrae.

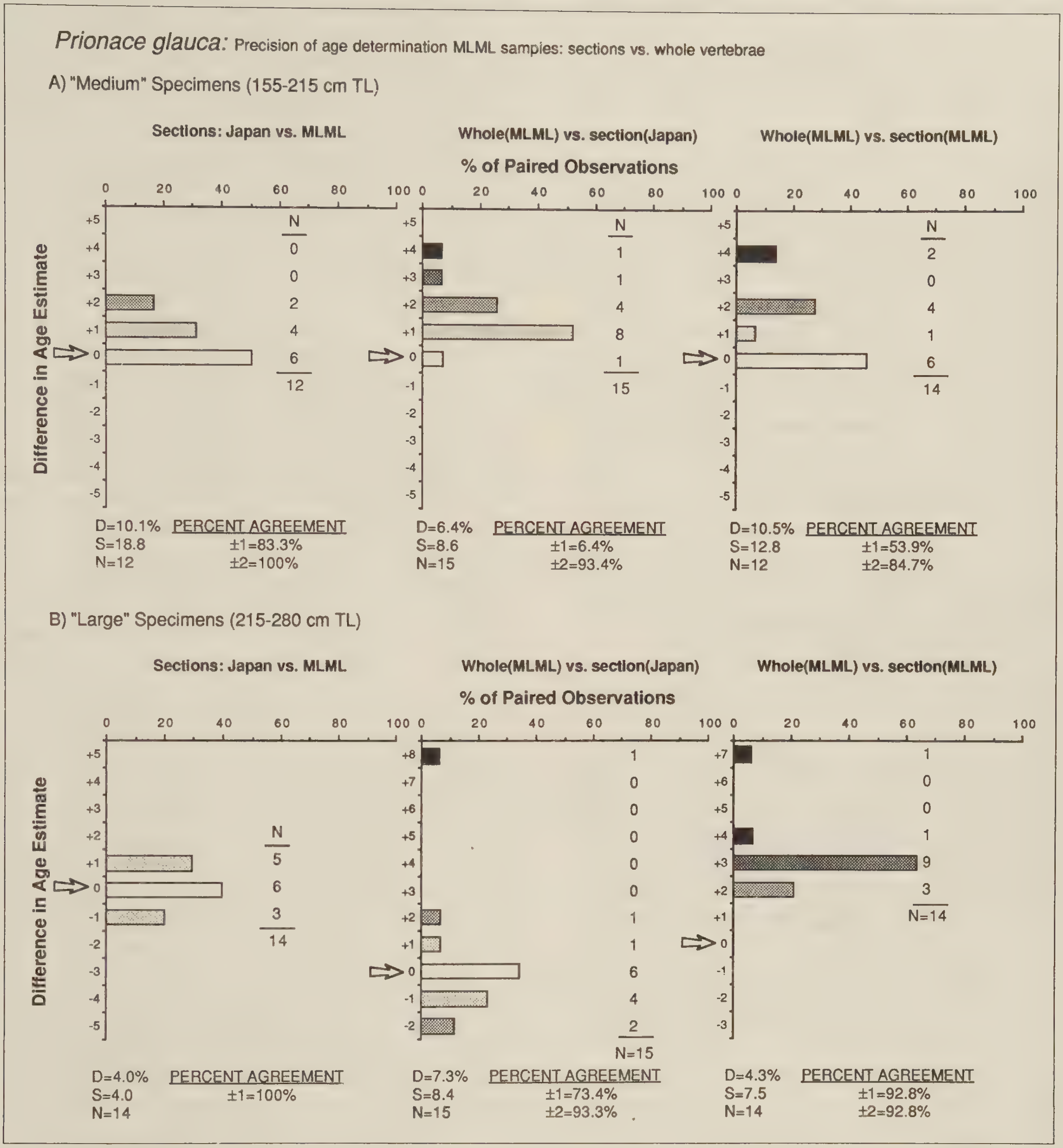

Figure 5.

Precision of age determination of female *Prionace glauca* from California. Sectioned age estimates are compared between Japanese and MLML counts, while whole vs. sectioned comparisons are between MLML versus Japanese counts and within MLML counts for (a) medium and (b) large specimens. Other details as explained for Figure 2.

Size-at-age data for combined sexes of blue sharks from Japan and California produced very similar curves (Fig. 6). The mean total lengths and 95% confidence intervals overlapped at all ages where sufficient comparable size data existed. For small blue sharks, which were estimated to be between 2 and 4 years old, D values ranged from 6.1 to 17.2%, which translates to age error estimates between 0.12 and 0.52 years. Medium sharks were estimated to be between 4 and 7 years old, and the relatively higher D values of 6.1 to 24.5% indicate age errors of 0.34 to 1.47

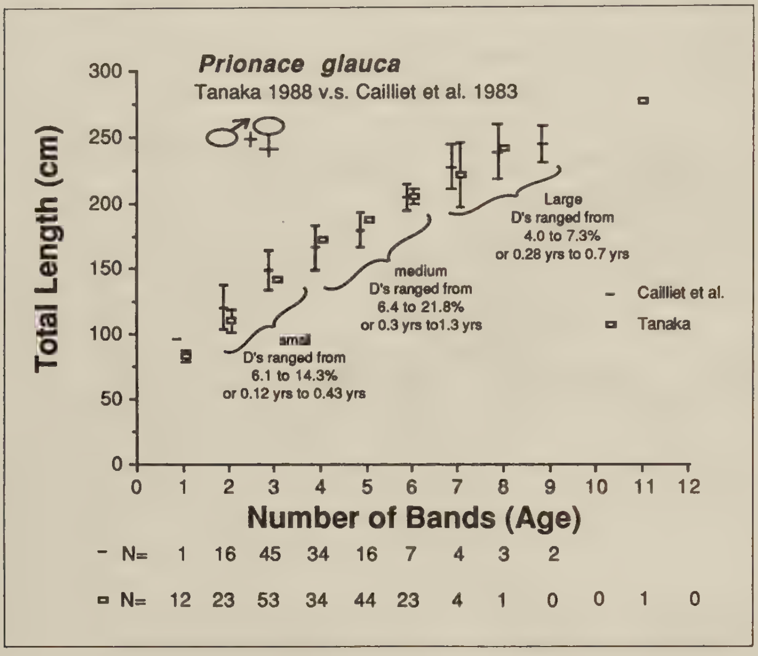

Figure 6.
Growth curves for male and female (combined) *Prionace glauca* from Japan (Tanaka 1984 data; open rectangles) and California (Cailliet et al. 1983b data, closed line), expressed as mean size at each age estimated from band counts). The vertical bars represent 95% confidence intervals, and "n" is the sample size at each age for each location. Ranges of percent error (D) values are presented for small, medium, and large blue sharks.

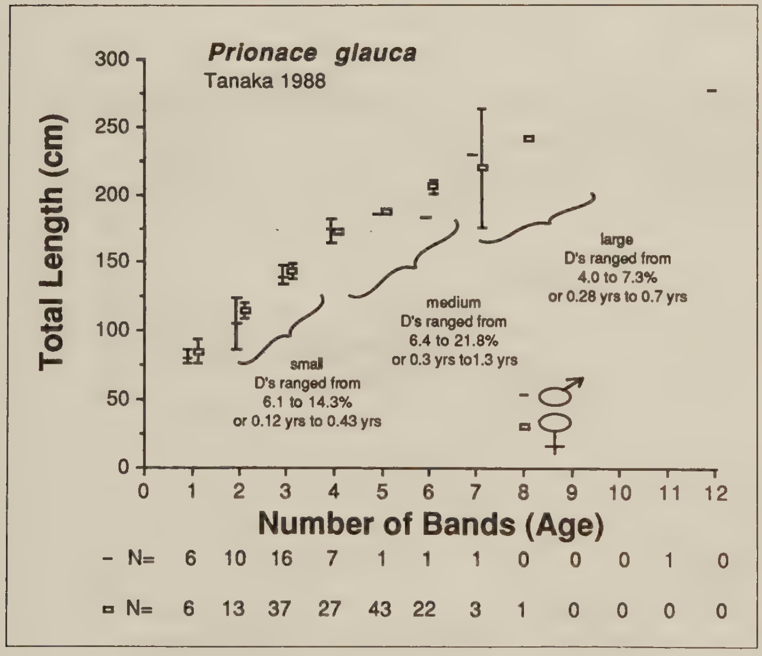

Figure 7.
Growth curves for Japanese *Prionace glauca* males (closed lines) and females (open rectangles) from Tanaka's (1984) samples, expressed as mean size at age estimated from band counts. Other details as explained for Figure 6.

years. Large sharks were between 7 and 9 years old, with D values ranging between 3.9% and 7.3%, translating to age errors of 0.27 to 0.70 years.

The size-at-age data for males and females in the Japanese blue shark sample, also produced very similar growth curves (Fig. 7). Mean total lengths and 95% confidence intervals overlapped at all ages where there were sufficient data for both sexes. An extremely broad confidence interval occurred only at age 7 for females, where the sample size was only 3. Small sample sizes for the larger sharks may account for the lack of sexual differences. The same range of D values is superimposed on this graph to acknowledge the potential error of between 0.12 and 1.47 years, depending upon the size and estimated age of blue sharks being considered.

The VBGF parameters calculated using FISHPARM on Tanaka's (1984) personal data set were within the range of values calculated by other researchers for blue sharks collected in other areas (Table 1). Asymptotic length (L_∞) estimates ranged between 242 and 375 cm TL for females and between 295 and 375 cm TL, for males (Cailliet et al. 1983b; Skomal 1989). In the North Atlantic Ocean study, male L_∞ values based on length frequency analysis were higher than those for females (Skomal 1988), while the opposite was true for L_∞ values based upon vertebrae. In the two Pacific Ocean studies (Cailliet et al. 1983b; this study), females reached larger L_∞ values. Likewise, K and t_0 values were similar among studies, locations, and sexes, and ranged from 0.10 to 0.25, and from −1.47 to −0.80. The broad confidence intervals, calculated in this study from Tanaka's (1984) large data base (Table 2), indicate that it would be difficult to detect any significant differences among these VBGF parameters between sexes or from different locations.

Discussion

When reader precision, inter-technique variability, means and confidence intervals of size at age, and goodness-of-fit of the VBGF are considered, it is difficult to make a very strong case that differences in growth characteristics occur in blue sharks between sexes or among geographically separate regions of the Pacific and Atlantic Oceans. Rather, these sources of error and imprecision cause sufficient variance to obscure any potential differences in VBGF parameters.

For the size range of blue sharks studied, percent errors were variable and ranged from low values for smaller sharks to high values for medium sharks. Sectioned centra of large sharks had higher precision values, probably because readers recognized that the finer growth rings were possibly annual. For medium size sharks, there was a difference in interpretation of these fine zones, with the Japanese counts always being lower than the MLML counts. Some of this difference might result from the experience that the MLML readers had with growth zones in larger leopard sharks, *Triakis semifasciata*, for which there is evidence from tag returns and tetracycline marking that the narrower growth zones are annual (Smith 1984).

Sectioned centra were generally more difficult to interpret, especially in older sharks. Both whole and sectioned centra from small size classes have fairly distinct growth zones. Growth in these younger sharks is relatively fast, hence the zones are broad and noticeable. However, with increased size, the centra have more numerous, fine growth zones, and sectioning makes these finer details easier to see. However, the interpretation of these zones is subject to debate.

To understand the differences, we need to know more about the temporal periodicity with which the growth zones are deposited (Cailliet et al. 1986). Unfortunately, to date, verification of growth zones in the blue shark is limited to size frequency analysis and some centrum edge analysis (Aasen 1966; Stevens 1975; Cailliet et al. 1983b; Cailliet and Bedford 1983; Skomal 1987). However, the shark tagging program of the Narragansett Laboratory, National Marine Fisheries Service (NMFS), has potential for providing growth information from their tagging and tetracycline marking validation studies (Skomal et al. 1988; Skomal 1989).

The mean size-at-age data produce growth curves which appear to have a shape that closely resembles a typical von Bertalanffy growth curve. The parameters calculated from Tanaka's (1984) data for western Pacific blue sharks indicate that there is a reasonable fit of the VBGF model to these data (Table 1). However, the confidence intervals around the L_∞ estimates, especially for males, are quite large. Nevertheless, these curves (Figs. 6, 7) appear similar to those in published accounts of blue shark growth elsewhere (Stevens 1975; Cailliet et al. 1983b; Tanaka 1984; Skomal et al. 1988; Skomal 1989).

These results raise questions about inter-population studies of fish growth. Some of these are discussed by Cailliet et al. (1990), in relation to growth comparisons among populations and species of *Mustelus*, for which sections of centra were necessary to accurately count growth zones. However, the growth zones are more easily read in small blue sharks, and most studies have used only whole centra impregnated with silver nitrate (Stevens 1975; Cailliet et al. 1983b). There is no reason to believe that the results on small sharks would differ significantly among studies in which different staining and sectioning techniques were used. For the older sharks, however, the use of different techniques might pose much more of a problem.

The possibility that inter-oceanic growth differences might occur cannot be eliminated. We have not done any real statistical tests between VBGFs from the different studies available, mainly because most of the studies done on blue sharks suffer from inadequate and biased samples. The VBGF parameters calculated in these studies most likely do not fully represent the growth of this species in either the Atlantic or Pacific Oceans. Blue sharks commonly reach lengths of 3 m TL in the Atlantic (Compagno 1984), but in the Pacific there are regionally smaller sizes common (Cailliet et al. 1983b; Tanaka 1984). Thus, significant inter-population growth differences may exist, but cannot be demonstrated with the data or methods available.

Movement patterns of blue sharks may also confound differential growth between geographic locations. Blue sharks taken by the Japanese in the western Pacific may at one time have been present off the shores of California. Researchers at the Narragansett NMFS Laboratory on Rhode Island have noted blue shark migrations of thousands of miles, from the east coast of the United States to the Caribbean and Mediterranean Seas. Any differences in growth of these migrating animals would be subject to the varying environmental conditions they encounter during these large scale movements. Seasonal patterns of migration might limit this effect, however, if individuals stayed within similar water masses and hence similar temperatures, salinities, and areas of food abundance.

The results of this study cast considerable doubt on the likelihood of detecting geographical differences in growth of the blue shark, with the data and methods currently available. Contrary to results found with *Mustelus manazo* (Cailliet et al. 1990), in which the VBGF did not adequately describe the length-at-age data available, it appears that blue sharks do exhibit growth which closely resembles the VBGF. However, sample and size biases, differences in preparation techniques, variable growth zone criteria, and low reader precision appear to be the major features which prevent us from concluding that blue sharks in different parts of the world's oceans have different growth characteristics.

Acknowledgments

We thank the numerous graduate students who worked on elasmobranch age and growth studies at Moss Landing Marine Laboratories, especially Jim Harvey, Dave Kusher, Linda Martin, Bruce Welden, and Patty Wolf, who helped process the blue shark centra and analyze the data used in this paper. Guillermo Moreno and Bill Hayden helped with computer analyses. Lynn McMasters did the illustrations. Gred Skomal provided accurate VBGF parameters from his and other studies and reviewed the manuscript. The United States–Japan Cooperative Research Project, funded by the National Science Foundation and the Japanese Society for the Promotion of Science, made the travel for this project possible. Wes Pratt thoroughly reviewed and edited this paper. The research was sponsored in part by NOAA, National Sea Grant College Program, Department of Commerce, under grant numbers 04-8-M01-189 and NA 80AA-D-00120; by the California Sea Grant College Program under project numbers R/F-57, R/NP-1-11C, R/F-81, R/F-84, and A/S-2; and in part by the California State Resources Agency. The U.S. Government is authorized to reproduce and distribute this information for governmental purposes.

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Age and Growth Studies on the Calcified Structures of Newborn Sharks in Laboratory Aquaria Using Tetracycline

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ABSTRACT

Japanese wobbegongs, *Orectolobus japonicus*, with known birth dates and neonate swell sharks, *Cephaloscyllium umbratile*, were kept in research tanks for periods between one and forty-one months to study their growth rates and the formation of growth bands in the cartilaginous tissues. The sharks were injected one to five times with oxytetracycline (OTC) at dosages between 20 and 80 mg/kg BW to mark the cartilaginous tissues. The growth rates of OTC injected sharks of both species were not significantly different from those of control sharks, and those of swell sharks were not affected by the dosages. OTC was incorporated in tissues on and after the 28th day following injection into the swell shark and was deposited mainly in the median zone of the centra and the periphery of other cartilaginous tissues in both species. The growth bands in the centra of wobbegongs usually formed annually in the spring. Two bands per year were observed in one wobbegong (spring and autumn). The formation time of the growth bands in the wobbegong sometimes varied with the growth rate of the centra rather than with time. Investigations of nonvertebral cartilaginous tissue revealed three growth bands in the upper jaw of one wobbegong. Other wobbegongs and swell sharks had no clear growth bands in their nonvertebral cartilaginous tissues. Growth rates of the centra ranged from 0.31 to 3.43 μm/day in wobbegongs and 1.61 to 4.51 μm/day in swell sharks.

Introduction

Age determination of fisheries resources is an essential component of life-history information and is used widely in stock assessments. Age of elasmobranch fishes has generally been estimated by studying growth bands in vertebral centra or dorsal spines (Kaganovskaia 1933; Ishiyama 1951a,b; Holden and Vince 1973; Ketchen 1975; Stevens 1975; Tanaka and Mizue 1979). These growth bands are formed by differences in the density of minerals, mainly calcium and phosphorus, across the structure as it forms over time (Cailliet and Radtke 1987). Special techniques must be used to clearly distinguish these zones of differing density to permit accurate counting or measuring of these growth bands. Cailliet et al. (1983) reviewed the different band-enhancement techniques used for analyzing the vertebral centra of elasmobranchs. Recently, the validity of these bands as time marks in vertebrae and spines has been studied in some sharks and rays (Gruber and Stout 1983; Pratt and Casey 1983; Smith 1984; Beamish and McFarlane 1985; Cailliet et al. 1986; Branstetter 1987; Brown and Gruber 1988; Cailliet 1990). However, the temporal periodicity of band formation is still unknown for most elasmobranchs.

The Japanese wobbegong, *Orectolobus japonicus*, and the swell shark, *Cephaloscyllium umbratile*, grow to about 1 m in total length. They are found in waters around southern Japan. The flesh of these sharks is used in fish cakes and boiled meal. Few biological studies have been carried out on these species (Iwamasa 1981; Taniuchi 1988). Since empirical information on age determination and calcium uptake is needed for elasmobranchs, I have examined the value of tetracycline-labeled calcified structures as age determination characters in the Japanese wobbegongs and swell sharks. I will try to determine if oxytetracycline (OTC) injection affects growth rate and if growth bands of centra are formed annually.

Materials and Methods

Eighteen wobbegongs were born in the Shimoda Floating Aquarium between 2 and 25 June 1983. The total lengths (TL) of the sharks ranged from 212 mm to 228 mm. Six

Table 1.
Dosage (mg/kg BW) of tetracycline administered to wobbegongs.

Shark identification	Date of OTC injection May 22 1984	Aug. 22 1984	Dec. 21 1984	May 22 1985	Sept. 21 1985
A	40	60	60		
C	40	60	40	40	40
E	60			60	

Table 2.
Dosage (mg/kg BW) of tetracycline administered to swell sharks.

Shark no.	Date of OTC injection May 15 1984	May 22 1985	Dec. 5 1986	Feb. 5 1987
84-A	40			
84-B	40			
84-C	80			
84-D	80			
84-E	60			
84-F	60			
85-A		20		
85-B		20		
85-C		40		
85-D		60		
86-A			40	
86-B			40	40
86-C			40	40
86-D			40	40
86-E			40	
86-F			40	
86-G			40	
86-H			40	
86-I			40	40
86-J			40	40
86-K			40	40
86-L			40	40
86-M			40	40

of the sharks were placed in research tanks at the Marine Science Museum, Tokai University, in March 1984. Three of these sharks were injected abdominally with oxytetracycline (OTC) (terramycin, injectable solution; Pfizer) at a dosage of 40 and 60 mg/kg body weight (BW) beginning in May 1984 (Table 1). The remaining three sharks were not injected but were kept in the same tank as controls for growth rate comparisons. These six sharks were identified individually by their body spots. The sharks remaining at the Shimoda Floating Aquarium were measured seven times after birth without individual identification by sex. The growth data were compared with those at Tokai University.

The swell sharks were caught with bottom shrimp trawls at depths between 150 m and 250 m in Suruga Bay in April 1984, 1985 and in November 1986 and were immediately transported to the Tokai University research tanks. They were acclimated for approximately one month. Ten of 12 surviving sharks kept in the same season of 1984 and 1985 were injected abdominally with OTC at varying dosages between 20 and 80 mg/kg BW to evaluate a proper dose (Table 2). The remaining two sharks were kept in the same tank as a control. Thirteen of 16 surviving sharks caught in 1986 were also injected abdominally with OTC at a dosage of 40 mg/kg BW on 5 December 1986 to examine the growth rates of the centra and the formation time of growth bands (Table 2). Eight of these sharks were again injected with a 40 mg/kg dose of OTC on 5 February 1987. The remaining three sharks were kept as a control. The total sample of 28 swell sharks were individually tagged.

Both wobbegongs and swell sharks in the Tokai University research tanks were kept at natural water temperatures and were fed 2 to 10 grams of fish meal per shark every Monday, Wednesday, and Friday. The water temperature was measured on these days. Sharks which died were measured and dissected. Skeletal tissues, including the vertebrae, upper and lower jaws, and pelvic and pectoral girdles, were dissected and fixed in 10% neutral formalin.

The wobbegongs in the Shimoda Floating Aquarium were also maintained at natural water temperatures and were fed 5 to 20 grams of fish meal per shark every three or four days. One of the sharks (SFA-1) which died on 23 July 1987 was fixed and preserved in 10% formalin, and then measured and dissected. The vertebral centra of the shark were then removed.

The skeletal tissues of the wobbegongs were sectioned by two methods: 1) Vertebral centra and other cartilaginous tissues were cut longitudinally and transversely with a revolving diamond saw, respectively, and were ground with wet stones. They were then attached to a transparent plastic plate (Takiron Plate) using a binding agent and further cut and ground to a thickness between 100 and 200 μm; 2) Skeletal tissues were decalcified with 5% formic acid, trimmed and sectioned to 100 to 200 μm thick with a freezing microtome. The skeletal tissues of the swell sharks were also trimmed and sectioned on a freezing microtome to a thickness of 100 to 200 μm without any decalcification.

The undecalcified OTC-labeled ground and microtomed sections from the skeletal tissues of the wobbegongs and swell sharks were observed and photographed using a fluorescent microscope. The OTC marks in the skeletal tissues were counted. The distances from the center of the centrum to the OTC marks and to the margin of the centrum were measured as the OTC radii (OTCr) and as the centrum radius (CR) using an ocular micrometer. The sections were then decalcified with 5% formic acid and stained with

Table 3.
Observed total length (OL, mm) and growth rate (GR, mm/day) of six wobbegongs kept in the research tanks between 22 May 1984 and 21 September 1985.

	Date of measurement								
Shark no.	May 22 1984		Aug. 22 1984		Dec. 21 1984		May 22 1985		Sept. 21 1985
A									
OL	375		418		439		416[a]		
GR		0.41		0.21					
B									
OL	375		425		482		516		555
GR		0.54		0.47		0.22		0.32	
C									
OL	370		411		476		552		563
GR		0.45		0.54		0.50		0.09	
D									
OL	365		380		413		420		438
GR		0.16		0.27		0.05		0.15	
E									
OL	395		425		461		476		465[b]
GR		0.33		0.30		0.10			
F									
OL	330		361		364		379		397
GR		0.34		0.02		0.10		0.15	

[a] Died on 15 March 1985.
[b] Died on 13 September 1985.

Mayer's hematoxylin. The microtome sections of the wobbegongs were also stained with hematoxylin. These stained sections were observed under transmitted light with dissecting and light microscopes. The distances from the center of the centrum to individual growth bands were measured as band radii (GBr). The growth band was defined as a darkened opaque band which stained deeply with hematoxylin.

The growth rate of the centrum was calculated by dividing the measured increase of the centrum from the OTC mark to the following OTC mark or the margin of centrum by the days of duration of the experiment, which is the period between OTC injection (not OTC incorporation) and the following OTC injection or death as noted by Gruber and Stout (1983). Back calculated length (BCL) at the OTC depositions and the formation of growth bands in the wobbegong were determined by the Dahl-Lea method using simple ratios (BCL = TL × OTCr/CR and TL × GBr/CR). The mathematical correlation between centrum radius and total length in the swell shark was calculated by the method of least squares.

Results

Wobbegongs

Growth Rate—OTC injected sharks A, C, and E died on 15 March 1985, 22 October 1987, and 13 September 1985, respectively. Growth rates of all captive sharks in the phases between the beginning of the experiment and 21 September 1985 ranged from 0.02 to 0.54 mm/day (Table 3). The growth rates of OTC injected sharks were not significantly different from those of the control sharks in each phase as measured by the Mann-Whitney *U*-test at $P > 0.2$. The *U* value was 4 in the first phase between May of 1984 and August of 1984 (the number of OTC injected sharks $n_1 = 3$, the number of controls $n_2 = 3$), 3 in the second phase between August of 1984 and December of 1984 ($n_1 = 2$, $n_2 = 4$), and 0 in the third ($n_1 = 1$, $n_2 = 4$) and fourth ($n_1 = 1$, $n_2 = 3$) phases. Five sharks, excluding shark A, exhibited varying growth rates of 49 to 182 mm per year from 22 May 1984 to 22 May 1985. The mean (M) and standard error of the mean (SEM) were 101.6 and 25.86 mm. The total lengths of sharks A and E at death decreased 23 and 11 mm, respectively, when compared with the last observed length. The mean and SEM of the total lengths of the nonexperimental sharks in the Shimoda Floating Aquarium were 367.0 ± 6.40 mm ($n = 10$) on 27 June 1984, and 459.8 ± 7.90 mm ($n = 5$) on 8 July 1985, respectively (Fig. 1). The growth of these sharks for about one year was 92.8 mm and seemed to be about the same as sharks kept in the research tanks. However, after June, 1985, the sharks in the Shimoda Floating Aquarium grew at a faster rate than those in the research tanks.

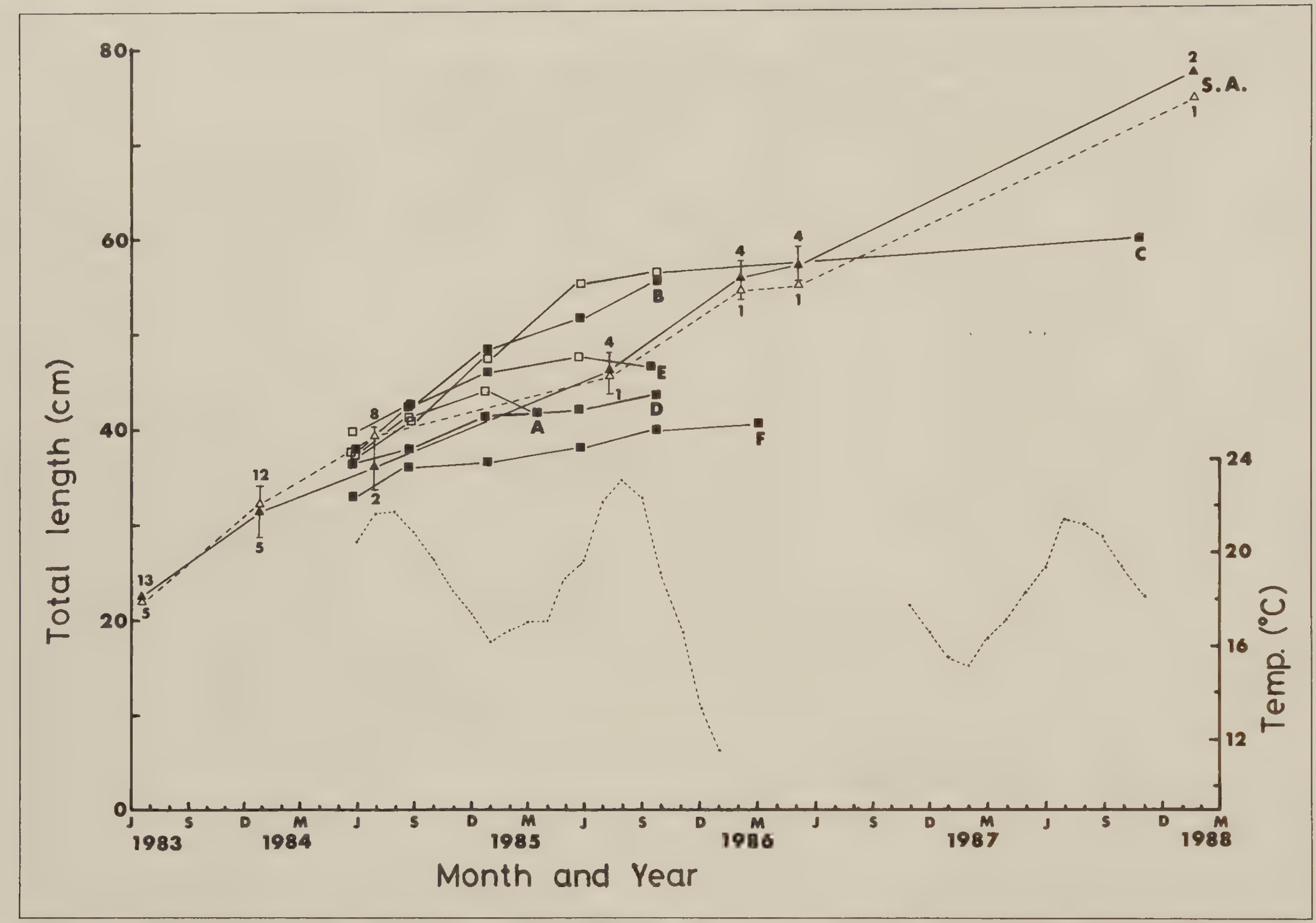

Figure 1.
Growth of wobbegongs kept in research tanks and in the Shimoda Floating Aquarium, compared to water temperature in the research tanks. Letters A to F indicate the six sharks. S.A. indicates the sharks in the Shimoda Floating Aquarium. The enclosed squares are only sharks which were measured. The open squares are sharks which were measured and injected with OTC. The closed and open triangles are the mean lengths of males and females, respectively. The vertical lines with triangles show the ranges of total lengths in both sexes. The numbers in the upper and lower sides of the line indicate the number of males and females, respectively. The dotted lines show water temperatures.

OTC Marks and Growth Bands—The centra of OTC injected shark A, which was alive for 21 months, had three growth bands and one OTC mark. Although the shark was injected with OTC three times, only one broad fluorescent band was observed in the centra. The centra of OTC injected shark C, which was alive for 53 months, had five growth bands and six OTC marks (Fig. 2A,C). The first, second, and fourth OTC marks were clear. The first, second, and third OTC marks fluoresced continually. The fourth OTC mark showed as a broad band. Shark C was injected with OTC five times. Six OTC marks appeared in the centra. The sixth OTC mark was indistinct. The centra of OTC injected shark E, which was alive for 27 months, had three growth bands and two wide and clear OTC marks (Fig. 2B,D). Control sharks F and SFA-1 were alive for 33 and 50 months respectively, and showed three and five growth bands in their centra, respectively.

The first and second growth bands in sharks A, C, and E were formed before the first OTC mark was deposited (Table 4, Fig. 3). The third and fourth growth bands in shark C were formed between the second and third OTC marks, and between the third and fourth OTC marks, respectively. The third growth band in shark E was formed between the first and second OTC marks. The radii of the first, second, and third growth bands were not different among the three OTC injected sharks respectively, and those values were almost equal to the radii in control shark F. The third, fourth, and fifth growth bands in shark C had smaller radii than those in shark SFA-1.

The first OTC mark had almost the same radius in all three sharks (Table 4, Fig. 3). For shark E, the radius of

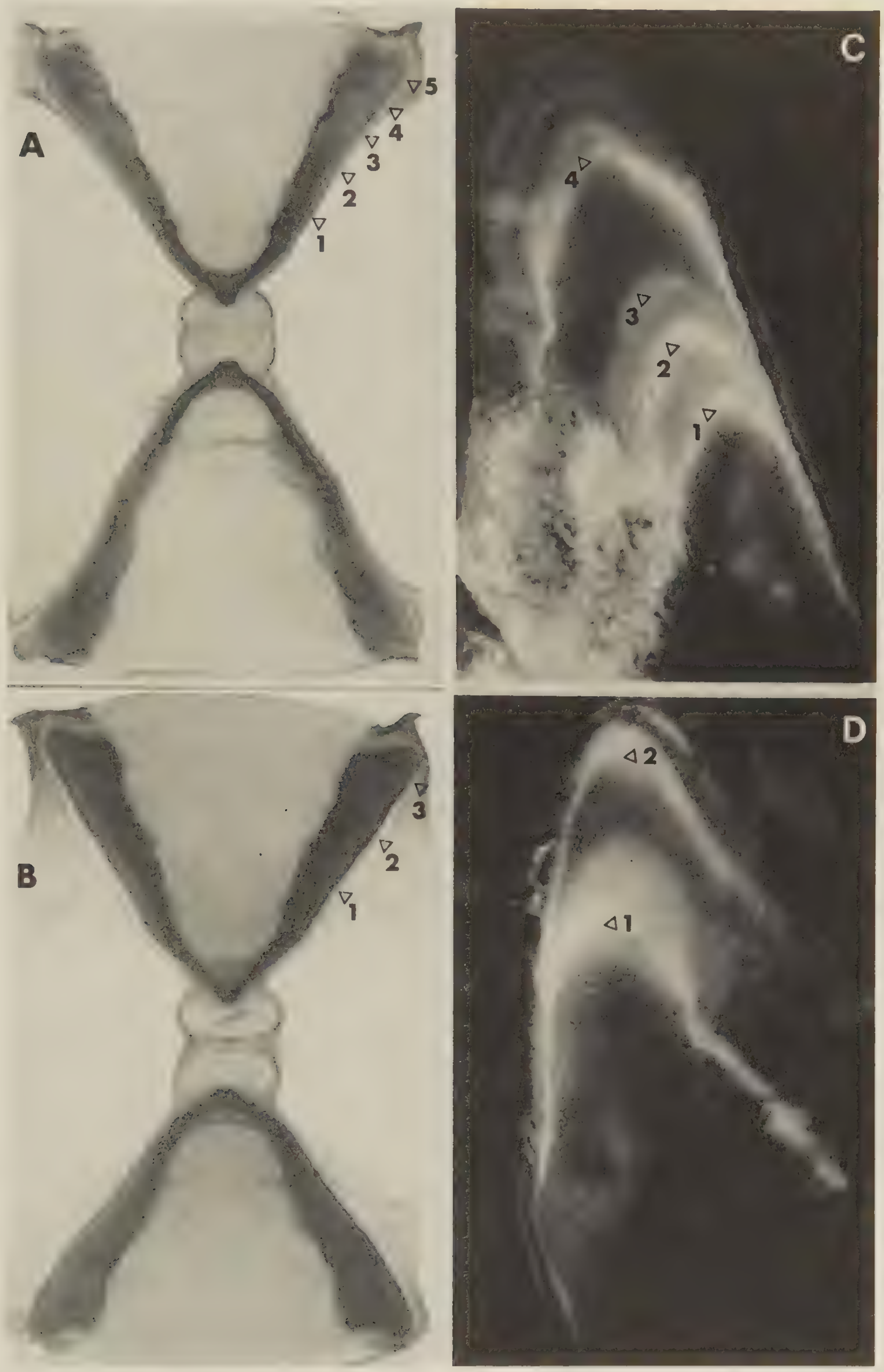

Figure 2.

Growth bands and OTC marks in the centra of wobbegongs: A) The centrum of shark C with five growth bands. B) The centrum of shark E with three growth bands. C) Six OTC marks in the centrum of shark C. D) Two OTC marks in the centrum of shark E.

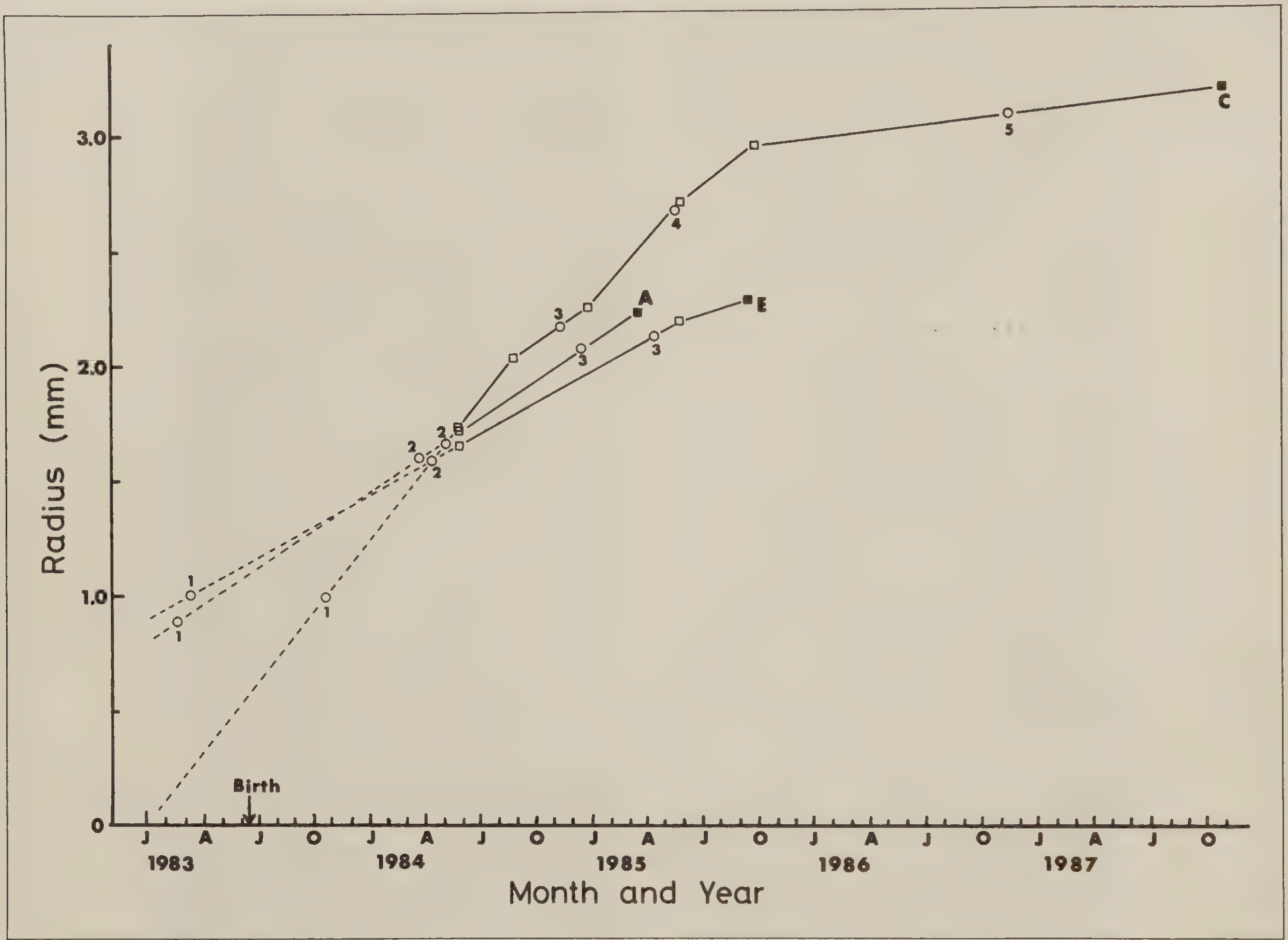

Figure 3.
Growth of the centra in wobbegongs A, C, and E. Open and closed squares show the radius of OTC marks and the centra at death, respectively. The open circles show the radius of growth bands. The number with open circles indicates the order of growth bands. The broken lines indicate estimated growth.

the OTC band resulting from the injection of 22 May 1985 (2.19 mm) was smaller than that of shark C (2.72 mm) but almost the same as the OTC radius of shark C (2.26 mm) observed on 21 December 1984 when the length (476 mm) of shark C was equal to that (476 mm) of shark E. The growth rate of the centra in shark A was 1.73 μm/day in the period from the first OTC injection to death. The growth rate of shark C ranged from 1.77 to 3.36 μm/day in the periods between OTC injections. The lowest value, 0.31 μm/day, occurred between the fifth OTC injection and death. In shark E, the growth rate was 1.45 μm/day between OTC injections, and 0.87 μm/day between the second OTC injection and death. The growth rate of the centra varied with body growth. Observed lengths of sharks A, C, and E at OTC injections were always larger than back calculated lengths, with differences between 9 and 59 mm (Tables 3, 4).

If the growth rates of the centra in shark A are the same before and after the first OTC injection, the first, second, and third growth bands must have been formed in February 1983, March 1984, and December 1984, respectively (Fig. 3). Similarly, the first to fifth growth bands in shark C were estimated to have been formed in October 1983, April 1984, November 1984, May 1985, and November 1986. The sixth OTC mark in shark C was probably deposited in November 1986, because the radius of the sixth OTC mark was the same as that of the fifth growth band. In shark E, the first, second, and third growth bands must have been formed in March 1983, April 1984, and April 1985, respectively (annually in the spring). The first growth band in sharks A and E was formed in the early spring of 1983, before birth, while that in shark C was formed in the autumn of 1983. The second growth band was formed in the spring of 1984 in all three sharks. The third growth band in sharks A and E was formed in

Table 4.
Radii (R, mm) from the center of each centrum to growth bands (GB) and oxytetracycline (OTC) marks, and back calculated length (BCL, mm) in wobbegongs.

	Wobbegong measurements										
	A		C		E		F		SFA-1		Date of measurement and OTC injection
	R	BCL	R	BCL	R	BCL	R	BCL	R	BCL	
1st GB	0.89	165	1.00	187	1.01	206	1.01	185	0.81	140	
2nd GB	1.60	297	1.66	309	1.60	324	1.53	283	1.61	278	
OTC	1.72	320	1.74	324	1.66	336					22 May 1984
OTC			2.05	382							22 August 1984
3rd GB	2.08	387	2.17	404	2.14	434	2.01	372	2.25	389	
OTC			2.26	422							21 December 1984
4th GB			2.69	502					2.95	510	
OTC			2.72	507	2.19	445					22 May 1985
OTC			2.97	554							21 September 1985
5th GB			3.09	577					3.58	618	
OTC			3.09	577							Unknown
At death	2.24	416[a]	3.21	598[a]	2.29	465[a]	2.19	405[a]	3.78	653[a]	

[a] Observed length at death.

the late autumn of 1984, while that in shark C was formed in the spring of 1985.

OTC deposition was also observed in the teeth and the peripheral portion of the upper and lower jaws and of the pectoral and pelvic girdles (Fig. 4A–D). Their peripheral portions are divided into small cartilaginous blocks which stained deeply with hematoxylin (Fig. 4E, F). In sharks A and E, only one OTC mark was seen in these nonvertebral cartilaginous tissues (Fig. 4A,C). However, those in shark C had two OTC marks (Fig. 4B, D).

Three growth bands were observed in the small block at the pointed end of the upper jaw in shark C (Fig. 4E). The small blocks at the peripheral portion of the lower jaw and of the pectoral and pelvic girdles had no clear growth band. In sharks A, E, and F, growth bands were not seen in the small blocks of these nonvertebral cartilaginous tissues (Fig. 4F).

Swell Sharks

Growth Rate—The sharks in the 1984 experiment died of natural causes after 28 to 97 days. The mean total length of the sharks at death was 245.2 ± 14.18 (SEM) mm. Two sharks showed a negative growth rate of −0.12 and −0.43 mm/day (Fig. 5, Table 5). The growth rates of the remaining four sharks with positive growth ranged between 0.10 and 0.36 mm/day. The growth rates among sharks injected at three different dosages were not significantly different by the Kruskal-Wallis test at $P > 0.20$ (H = 0.857). The water temperature in June and July 1984 was 21.0 ± 0.25 (SEM) °C.

The 1985 shark samples died on the 48th and 54th days. Only shark 85-D was kept continually. The mean total length of the sharks was 323.5 ± 20.89 (SEM) mm. Sharks 85-A and D showed a negative growth of −0.20 and −0.30 mm/day, respectively (Fig. 5, Table 5). The growth rates of the remaining four sharks ranged between 0.07 and 0.28 mm/day. The growth rates of the control sharks were higher than those of the OTC injected sharks. The mean water temperature in June and July 1985 was 21.0 ± 0.40 (SEM) °C and not significantly different from that in 1984 ($t = 1.289$, $P > 0.20$).

The growth rates of the six sharks in 1984 were determined to be not significantly different from those of the six sharks in 1985, by the Mann-Whitney U-test at $P > 0.10$ ($U = 16$). In 1984 and 1985, the growth rates among control sharks, OTC injected sharks at a 20 mg/kg dose, those at a 40 mg/kg dose, those at a 60 mg/kg dose, and those at a 80 mg/kg dose were not significantly different by the Kruskal-Wallis test at $P > 0.20$ ($H = 5.78$, $K = 4$). This suggests that the dosage differences between 20 and 80 mg/kg did not affect the body growth rate.

In the 1986 experiment, shark 86-A died after 17 days, and 11 of 15 sharks died between February 11 and March 5, 1987. The mean total length of the sharks was 300.2 ± 11.52 (SEM) mm (Table 5). Seven of the 11 sharks that died had been given a second OTC injection. During the same period, two of the four sharks which were given the first OTC injection but not the second OTC injection, and two of three control sharks also died. The mortality of the sharks with two OTC injections was not significantly different from that of the sharks with only one OTC

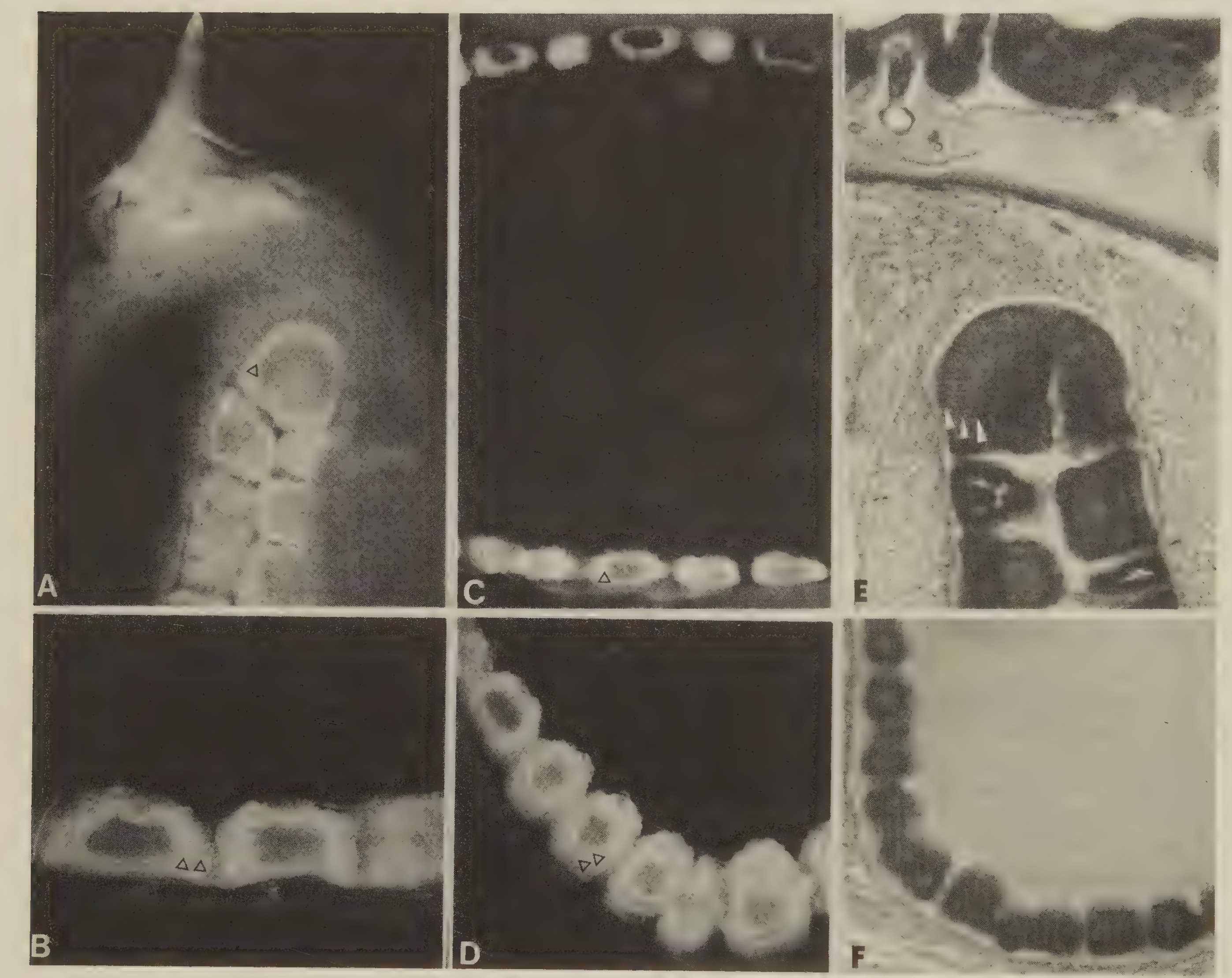

Figure 4.
Tooth and nonvertebral cartilaginous tissues showing areas of OTC deposition and hematoxylin staining in wobbegongs: A) The margin of the upper jaw with OTC deposition in shark A. B) The peripheral portion of the lower jaw in shark C, in which two OTC marks can be observed. C) The peripheral portion of the pelvic girdle with OTC deposition in shark E. D) The small blocks at the peripheral portion of the pectoral girdle of shark C with two OTC marks. E) The tooth and upper jaw stained with hematoxylin in shark C, in which three growth bands can be observed. F) The peripheral portion of the pectoral girdle in shark A, in which small blocks are deeply stained with hematoxylin.

injection by the Fisher's exact probability test at $P = 0.236$. This suggests that the second OTC injection did not contribute to the high mortality. The cause of death was unknown. The lengths of the dead sharks were shorter than when measured live on 5 February 1987 (Fig. 5). The bodies of the sharks shrank between 3.4 and 7.5 percent in length prior to death. Between 5 December 1986 and 5 February 1987, the growth rates of these sharks, excluding shark 86-A, ranged from 0.37 to 0.77 mm/day (M ± SEM = 0.59 ± 0.030 mm/day), and were higher than those in the 1984 and 1985 experiments. Shark 86-A, which died 17 days after the beginning of the experiment, showed negative growth. The growth rates of three control sharks in the 1986 experiment were not significantly

Figure 5.
Growth of swell sharks compared to the water temperature in the research tanks. The closed triangles, open and closed circles indicate the sharks in 1984, 1985, and 1986, respectively. The letters indicate individual sharks. The broken lines show the water temperatures.

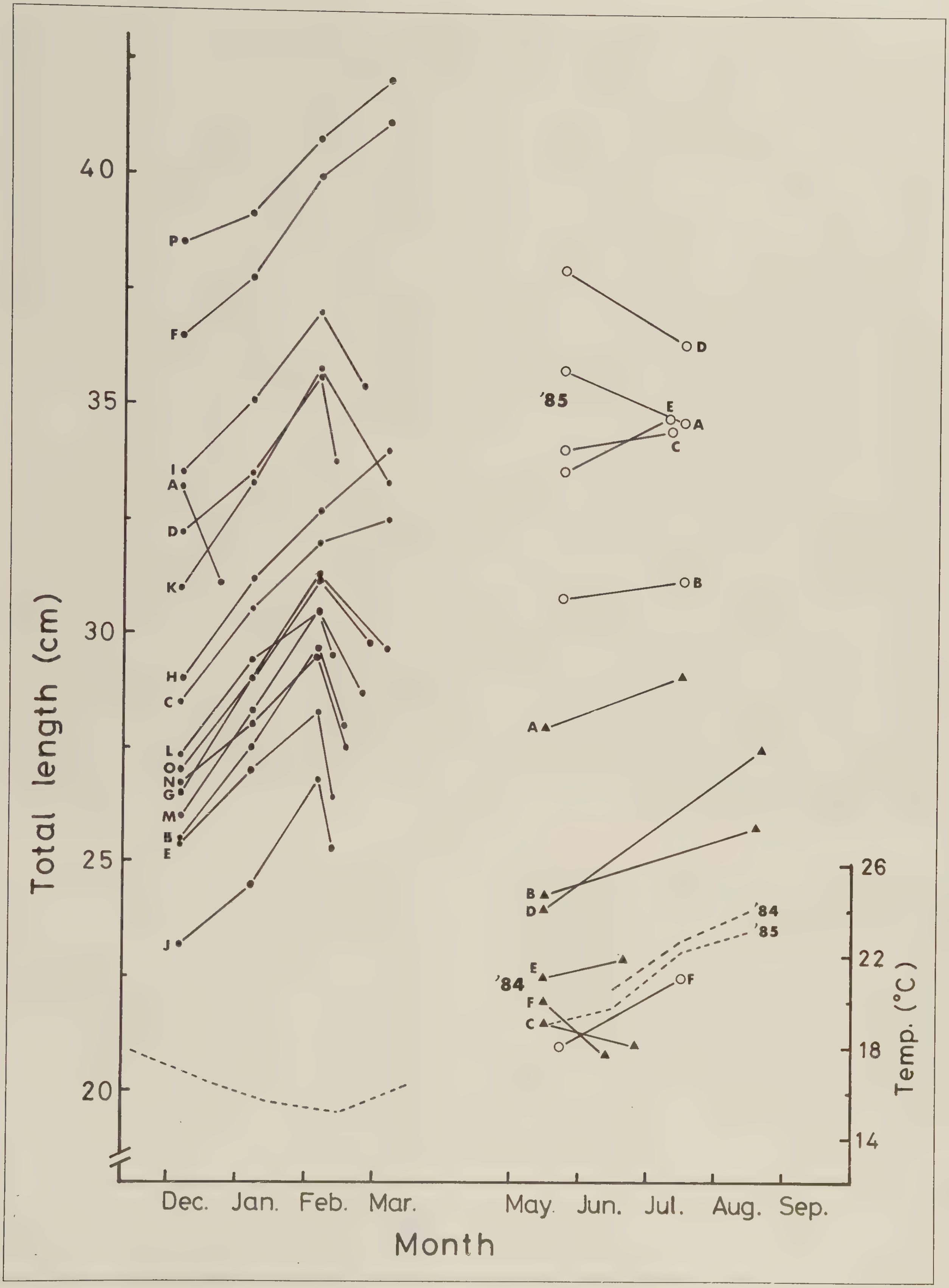
Total length (cm)
40
35
30
25
20
P
F
I
A
D
K
H
C
L
O
N
G
M
B
E
J
'85
D
E
A
C
B
A
B
D
'84
E
F
C
F
'84
'85
26
22
18
14
Temp. (°C)
Dec.
Jan.
Feb.
Mar.
May.
Jun.
Jul.
Aug.
Sep.
Month

Table 5.

The growth rates of bodies and centra in swell sharks. The growth rates of bodies in the sharks of 1986 were calculated from the growth between 5 December 1986 and 5 February 1987.

Shark no.	Duration (days)	Total length at death (mm)	Centrum radius at death (mm)	Growth rate of body (mm/day)	Growth rate of centrum (μm/day)
84-A	61	291	1.21	0.18	4.34
84-B	95	258	1.08	0.10	3.84
84-C	41	210	0.78	−0.12	4.51
84-D	97	275	1.14	0.36	2.94
84-E	36	229	0.93	0.11	1.67
84-F	28	208	0.80	−0.43	1.61
85-A	54	347	1.70	−0.20	
85-B	54	312	1.31	0.07	
85-C	48	345	1.84	0.08	2.31
85-D	54	364[a]		−0.30	
85-E	48	348	1.53	0.25	
85-F	54	225	0.88	0.28	
86-A	17	311	1.50	−1.24	
86-B	71	280	1.13	0.67	3.17
86-C	62	320[b]		0.56	
86-D	69	338	1.34	0.54	2.25
86-E	68	264	1.07	0.47	2.35
86-F	62	400[b]		0.56	
86-G	84	298	1.04	0.77	2.26
86-H	62	327[b]		0.60	
86-I	81	354	1.40	0.56	2.96
86-J	68	253	1.05	0.58	2.50
86-K	91	333	1.36	0.77	2.44
86-L	68	295	1.12	0.52	2.65
86-M	81	287	1.10	0.73	2.65
86-N	74	275	1.09	0.45	
86-O	91	297	1.14	0.68	
86-P	62	408[b]		0.37	

[a] Observed length on 15 July 1985.
[b] Observed length on 5 February 1987.

different from those of 12 OTC-injected sharks except for shark 86-A which displayed negative growth (Mann-Whitney *U*-test at $P>0.10$ [$U = 9$]). The mean water temperature between December 1986 and February 1987 was 15.8 ± 0.12 (SEM) °C and lower than in 1984 and 1985.

OTC Marks and Growth Bands—The centra of the OTC injected sharks, excluding sharks 85-A, -B, and 86-A, had one OTC mark (Fig. 6A, B). In some of the sharks, OTC was deposited as a broad fluorescent band. Sharks 85-A and -B, which were injected with a 20 mg/kg dose of OTC, had no OTC mark in their centra. The centra of shark 86-A, which died 17 days after OTC injection, had no OTC mark. In the 1986 experiment, although seven sharks died within 28 days of the second OTC injection (Tables 2, 5), the second OTC mark did not form in their centra. Sharks 84-E and -F died 36 and 28 days after OTC injection; each had one clear OTC mark in the margin. This suggests that OTC is incorporated in the centra on and after the 28th day following injection.

In the 1984 experiment, the growth rates of centra having a dosage of 60 mg/kg were slower than those of centra having a dosage of 40 and 80 mg/kg. The growth rates of the centra of OTC injected sharks in the 1984 experiment ranged between 1.61 and 4.51 μm/day (M ± SEM = 3.15 ± 0.527 μm/day), and those in the 1986 experiment ranged between 2.25 and 3.17 μm/day (2.58 ± 0.105 μm/day). The growth rates measured in 1984 were not significantly different from those seen in 1986 when compared by the Mann-Whitney *U*-test ($U = 20$, $n_1 = 6$, $n_2 = 9$, $P>0.10$). However, there was a greater variation in growth rate in 1984 than in 1986 ($F = 16.85$, $n_1 = 6$, $n_2 = 9$, $P<0.001$).

The centra of those sharks, excluding five sharks; 85-D, 86-C, -F, -H, and -P, which were kept continually, had one or two growth bands (Fig. 6C, D). The radius of the first growth band ranged between 0.52 and 0.72 mm (M ± SEM = 0.64 ± 0.011 mm). The first growth band was

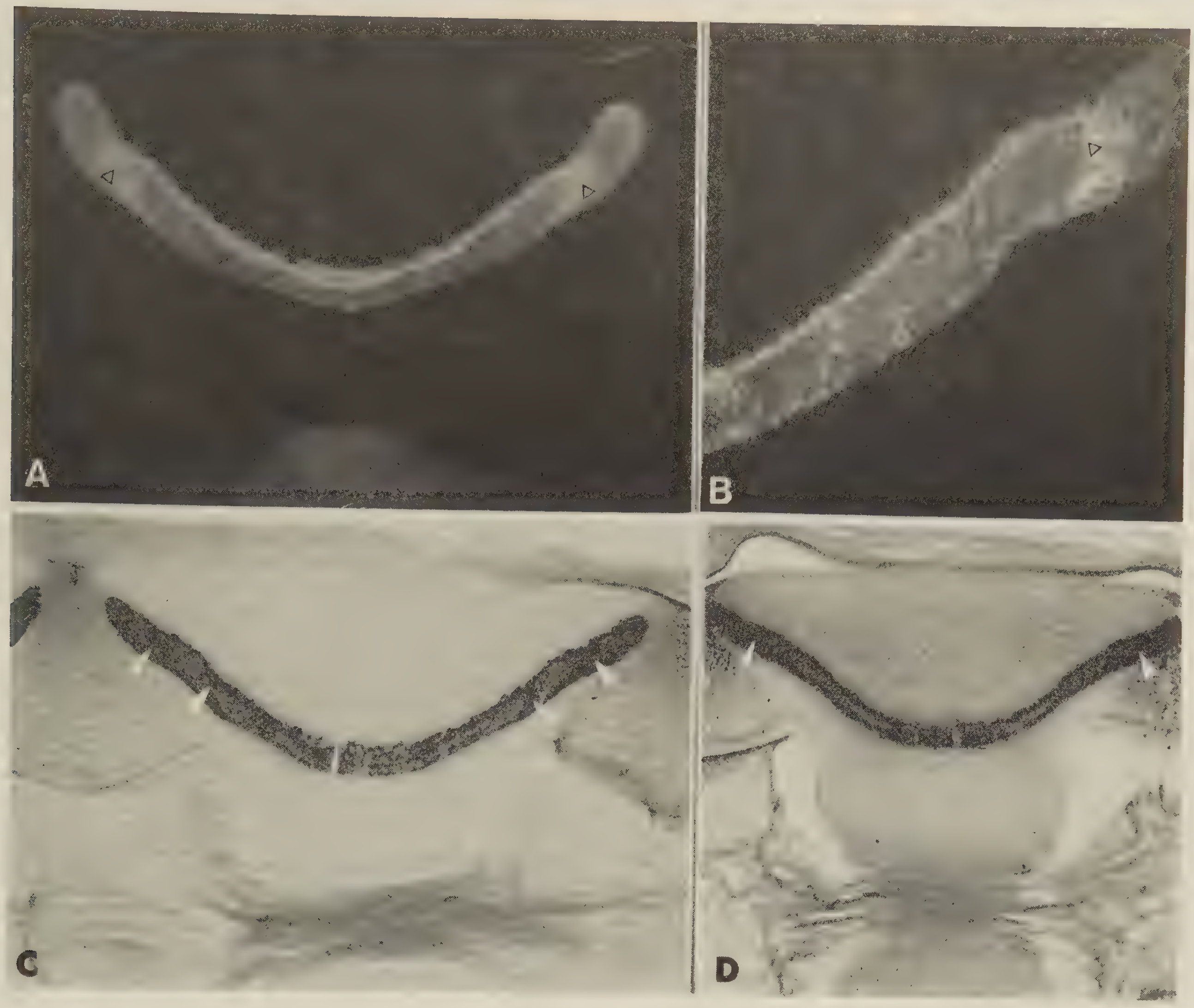

Figure 6.
The centra of the swell sharks: A) The OTC mark in the centrum of shark 84-D, injected with OTC at a dosage of 80 mg/kg BW. B) The OTC mark in the centrum of shark 86-G, injected with OTC at a dosage of 40 mg/kg BW. C) The centrum of shark 84-A (291 mm TL) with two growth bands. D) The centrum of shark 86-E (264 mm TL) with one growth band.

formed before OTC deposition. A second growth band was observed in ten sharks, 84-A, 85-A, -B, -C, -E, and 86-A, -B, -D, -I, -K. The radius of the second growth band ranged between 0.91 and 1.09 mm (M ± SEM = 1.01 ± 0.024 mm). The relationship between the centrum radius (CR) and total length (TL) may be represented by:

$$\mathrm{TL} = 256 \times \mathrm{CR}^{0.675} \qquad n = 23,\ r = 0.924,$$

where n is the number of sharks and r is the correlation coefficient. If the mean radii of the first and second growth bands are substituted in this formula, formation of the first and second growth bands calculate to be 189 and 258 mm TL, respectively. The formation time of the growth bands could not be determined exactly.

OTC deposition was also observed in the teeth and the peripheral portion of nonvertebral cartilaginous tissues. The peripheral portion consisted of small blocks as in the wobbegong. The small block had one broad OTC mark. The peripheral portion stained deeply with hematoxylin. A growth band was not seen in the small blocks.

Discussion

Oxytetracycline has often been used for age validation studies in elasmobranchs, but the influence of the administration of OTC on growth rates and mortality has not been investigated. In this study, somatic growth rates of wobbegongs were not affected by OTC at a dosage of

40 and 60 mg/kg BW. In the swell sharks, the growth rates of the body in length and the centra in radius, and mortality were not affected by the presence of OTC at dosages between 20 and 80 mg/kg BW. However, the growth rates of the body and centra of the swell sharks in the 1984 and 1985 experiments were more variable than those seen in 1986. This may have been caused by water temperatures and length of the experiment. The water temperatures in the 1984 and 1985 experiments were higher than those in 1986. The temperatures in 1986 appeared to be more suitable for swell sharks than those in 1984 and 1985, because they generally inhabit the sea bottom between 150 and 250 m where temperatures range from approximately 13 to 18°C. The higher experimental temperatures in 1984 and 1985 may have exerted stress on the sharks and have affected their growth rates. The lengths of the 1984 and 1985 experiments were more varied than those of 1986. The shorter the length of the experiment, the more influence the period of OTC incorporation has on centrum growth.

Gruber and Stout (1983), Smith (1984), Beamish and McFarlane (1985), and Branstetter (1987) using tetracycline methodology reported that the bands in centra or dorsal spines are formed annually in sharks they examined. Recently, Brown and Gruber (1988) validated that the circuli in the intermedialia of the centrum of the lemon shark, *Negaprion brevirostris*, are deposited following a lunar cycle. My OTC injection study did not clearly show the periodic formation of the growth bands in the wobbegong. The growth bands that stained deeply with hematoxylin were formed in the spring and/or autumn. I hypothesize that the differences in the formation time of the first growth band between sharks A and E and shark C probably occur because the growth rates of the centra were the same before and after the first OTC injection (Fig. 3). As the growth rate of the centra of shark C was much faster than that of sharks A and E, the first growth band of shark C was formed later than that of sharks A and E. The radius of the first growth band and the length at birth in these sharks were almost the same (Figs. 1, 3). This suggests that the first growth bands of wobbegongs are formed in the same season, probably in the spring. The differences in the formation time of the third growth band of three sharks seemed to be caused by the differences in the growth rates of their centra. The faster the growth rate of the centra, the shorter the formation time interval between the second and third growth bands. Shark C had only one growth band during the last two years when the growth rate of the centra was much slower. Thus, it was observed that faster growth rate of the centra was accompanied by the formation of more bands. Generally, in elasmobranchs, a positive correlation between centrum growth and body growth has been observed. Body growth probably influences calcium metabolism in the centra. Although the body growth in wild wobbegongs is unknown, if it is similar to the growth of shark E which had annual growth bands, the growth bands in the centra of wild wobbegongs are probably formed annually in the spring. Further work must be done to explain band periodicity. Thus, age and growth of elasmobranch fishes would need to be estimated by investigating growth bands in centra or spines together with other methods, such as analysis of size frequency and tag recapture as reported by Pratt and Casey (1983).

OTC uptake varied in the centra of wobbegongs as it did in the age validation study of leopard sharks, *Triakis semifasciata*, by Smith (1984). Although sharks A and C were injected with OTC three times in 1984, shark A had one broad fluorescent band and shark C had several discrete fluorescent bands. OTC from the first and second injections of shark A seemed to continue to deposit in the centra for three and four months, respectively, and to have combined. Moreover, OTC injected in May into sharks C and E and in August into shark C formed clear fluorescent bands. September and December injections of shark C produced indistinct fluorescent bands. The clearness and width of OTC marks appear to be affected by the condition of calcification of the centrum rather than the dosage of OTC, because OTC deposition was often quite different in sharks which had been given the same dosage. These variations of OTC uptake could have been caused by a changing calcium metabolism, which is influenced in turn by internal factors such as health, nutrition, size, stage of maturity, and environmental factors such as temperature and light. Electron microprobe analysis of calcium and phosphorus weight-fraction concentrations across the surface of sectioned vertebral centra from gray reef sharks, *Carcharhinus amblyrhynchos*, and common thresher sharks, *Alopias vulpinus*, shows variation in the height and spacing of their peaks (Cailliet and Radtke 1987). This suggests that the calcium metabolism in the vertebral centra of each shark is affected by several unresolved factors.

OTC-injected wobbegongs and swell sharks had one or two fluorescent marks in their teeth and in the small blocks of their other nonvertebral cartilaginous tissues. Each small block seems to consist of chondrocytes which exhibit cartilaginous calcification. Three growth bands were seen in the small block in the upper jaw of shark C. Other wobbegongs and swell sharks had no clear growth bands in their small blocks. As the small blocks of these tissues seemed to show an appositional growth, they may be worth studying for their usefulness as an age determination character in the future.

OTC was deposited in the cartilaginous tissues of the swell shark on and after the 28th day following injection. Gruber and Stout (1983) reported that tetracycline injected intermuscularly was incorporated in the centra of lemon sharks within 30 days. A leopard shark, which was injected with OTC intraperitoneally, had a fluorescent mark in the vertebrae within one month (Smith 1984). Branstetter (1987), however, reported 36–72 hours as an incorporation time in *Carcharhinus limbatus* and *Rhizoprionodon terraenovae* which were injected intraperitoneally with OTC. The differences in OTC incorporation times may be caused by differences in seasonal calcification or species differences.

Holden and Vince (1973) recommended a tetracycline dosage of 25 mg/kg BW. Smith (1984), Beamish and McFarlane (1985), and Branstetter (1987) have also used dosages of 25 mg/kg for sharks. Gruber and Stout (1983) and Brown and Gruber (1988) injected tetracycline at a lower dosage of 12.5 mg/kg into lemon sharks. They have observed OTC marks in all cases. Studies by Smith (1984) and Beamish and McFarlane (1985) showed that 64 and 66 percent of recaptured sharks which had been injected with OTC had a fluorescent mark. Results of this OTC injection study of swell sharks show that OTC at a dosage of 20 mg/kg did not deposit in cartilaginous tissues, but higher dosages did produce broad but readable fluorescent bands. As with wobbegongs, OTC uptake in swell sharks probably differs with size of the shark and timing of the injection.

Acknowledgments

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The Care and Maintenance of Elasmobranchs in Controlled Environments[1]

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ABSTRACT

The difficulties of studying free-ranging sharks, skates, and rays are obvious and it is logical that these animals can be studied more efficiently and effectively in an experimental facility. As basic knowledge of elasmobranchs increases so does the ability to maintain these animals for study in controlled environments for extended periods of time. It is important, however, that animals maintained in these environments exhibit as close to ''normal'' activity as possible.

Our increasing understanding of the life history of elasmobranchs, coupled with technological advances and improved facility designs, allows researchers increased opportunities to study these animals in a more detailed and cost effective manner. Elasmobranchs of many species are being maintained for extended periods and, in some species, through many generations (Uchida et al. 1990). Some, such as the white shark, *Carcharodon carcharias*, and the manta rays, *Manta birostris* and *M. hamiltoni*, continue to elude captive management; but efforts to understand the specific needs of selected species continue. With increased understanding these, too, will someday be available for detailed study. Many quality facilities exist around the world for the controlled study of elasmobranchs and most have ongoing programs of study. The use of these facilities by researchers are generally welcomed and encouraged.

Introduction

The care and maintenance of elasmobranchs in captive environments for research and educational purposes is not a new endeavor. The successful management of juvenile or smaller members of many species of sharks, skates, and rays has been well documented (Gruber and Keyes 1981; Clark 1963a, b; Essapian 1962; Gohar and Mazhar 1964; Graeber 1974; Keyes 1979; Kistnasamy 1974; Klay 1977; Weihs et al. 1981). However, the maintenance success of larger, more pelagic or epipelagic species has been, until recent years, far from successful. Information accumulated from those species which had been maintained for periods of months, or even years under marginal conditions, may be of questionable value from a research standpoint (Martini 1978). Clark (1963b) demonstrated, in her census of sharks in captive environments, that pelagic elasmobranchs were being maintained for periods of one to four years with most falling considerably short of this and surviving from only a few weeks to several months. While only a few additions may be made to a list of new species being maintained in captivity, in the last few years a significant improvement has occurred in the long term survival of most elasmobranchs (Uchida et al. 1990).

Numerous factors have contributed to this improved survivability. The most notable of these will be discussed.

Capture and Transport

The proper capture and handling of any elasmobranch can affect not only the survivability of the animal but influence future research results as well. During any capture and transport procedure the minimizing of stress on the animal is paramount. Elimination of all stress is impossible. Even the slightest handling may elicit a stress response (Rasmussen and Rasmussen 1967).

The standard techniques for capture of large sharks have been the use of longlines, setlines, and standard hook and line fishing. In commercial fisheries longlines or set lines may be submerged for many hours, but proper technique for live capture requires very short sets of not more than one to two hours duration. Extra long leaders extending

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[1] Sea World of Florida Technical Contribution No. 8809-F.

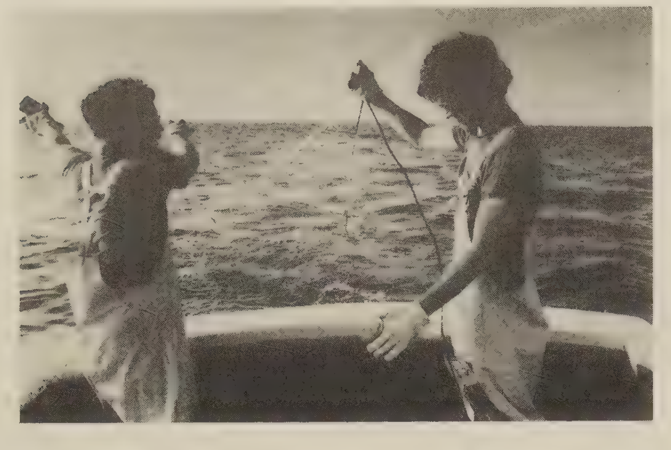

Figure 1.
Longline fishing operations have been used successfully for many years and are an effective technique for obtaining both large and small sharks and rays.

from the mainline will act as a leash and allow a rather abbreviated swimming pattern after the fish is hooked (Fig. 1).

Proper choice and rigging of the gear will also assist in removal of the hook and will minimize damage to the jaw. A large loop at the end of the hook shank will permit a quick cut to sever the leader from the hook. A smooth eye at the end of the hook shank will help the hook to slip freely through the jaw, thus eliminating damage from the barb (Fig. 2).

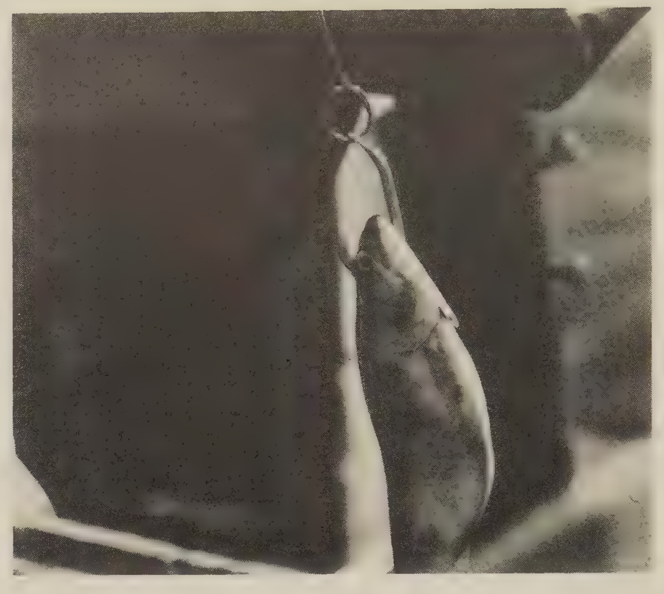

Figure 2.
A large loop on the longline leader at the hook will permit an easy cut to sever the leader from the hook, allowing easy removal from the jaw. Note also the smooth eye in the hook shank.

Hook and line fishing has the distinct advantage of immediate retrieval of the catch. For those field experiments requiring rapid evaluation of a "normal" shark, this may be the method of choice (Murru and Case 1984;

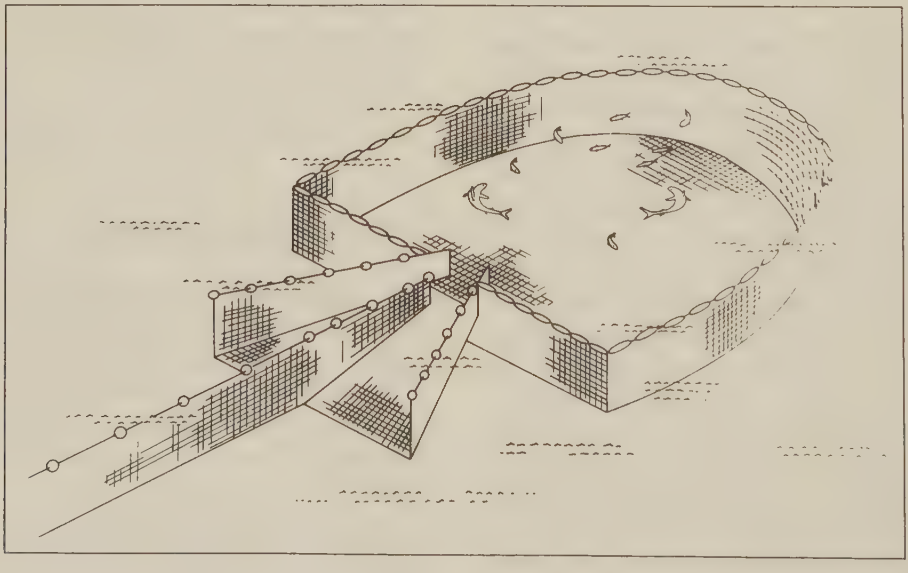

Figure 3.
Pen nets similar to that shown in this diagram are very effective in concentrating fish without damage. They are typically set in coastal areas along known migration routes or perpendicular to a longshore current.

Rasmussen and Rasmussen 1967). A very heavy pole and line must be used to pull the shark to the aquarist or researcher in the shortest possible time.

Several other techniques have also been used successfully. The use of pound nets, and barrier or pen nets have the advantage of not damaging the specimen in any way. These nets are generally set up within an area of a known migration route or in a current and consist of large walls of net or fence which direct fish along its length, terminating within a large compound. The fisherman simply concentrates his catch (Fig. 3). The disadvantage to this system is crowding within the holding area or compound unless it is emptied regularly. Also, considerable damage to the nets and specimens could result should a large shark or other large animal enter the net.

Perhaps the best devices for quick capture of smaller elasmobranchs are the cast net and the rigid hoop. Both of these must generally be used in shallow water. The cast net depends largely on the expertise of the thrower, and, because the specimen becomes entangled in the nylon mesh, it can cause considerable abrasion to the fish. The rigid hoop is composed of two steel hoops, top and bottom, with a heavy wire or plastic mesh for sides. It is generally about 1–1.5 m in diameter and 0.5 m in height. The hoop is thrown over the shark in shallow water and with practice is surprisingly effective.

Other techniques exist and have been tried, the most unsuccessful of which is the gill net. For obtaining healthy specimens and keeping stress to a minimum, this equipment should be avoided. While it is certainly effective, the damage and loss of specimens is rarely worth the use of this fishing technique.

Careful handling of the specimen is very important in maintaining proper health. Sharks, skates, and rays possess varying amounts of loosely organized internal connective tissue and little skeletal support for protection of organ systems (Daniel 1922; Clark 1963b). The careless removal of the fish from the water may be severely damaging, especially with the larger, heavier sharks. Body weight should be evenly supported during removal or transferral. A net may serve this purpose; however, net material can be abrasive and mesh size in relation to shark size is important.

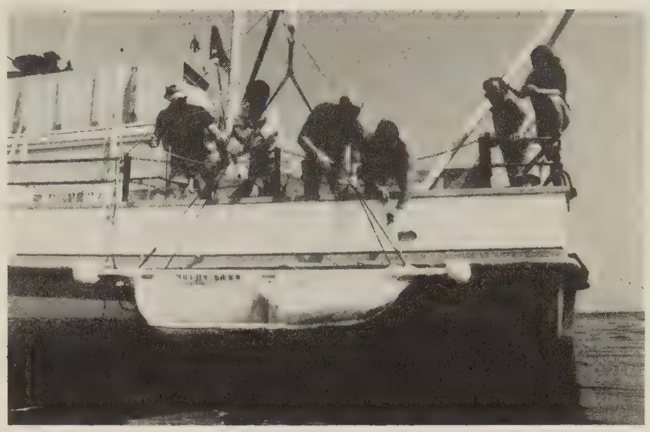

Figure 4.
Since sharks possess varying amounts of loosely organized internal connective tissue, supporting their weight with a stretcher-like apparatus as shown is important.

A stretcher apparatus works best for medium to large sharks. Poles or rigid sides aid in lifting ability and keep the stretcher and shark evenly supported. Drainage holes, or a highly porous material, will also assist in lifting only the fish and not additional water weight (Fig. 4).

The life support system used during transport may vary in size but contains essentially these elements: a recirculating water system, either open (continuously bringing in and disposing of fresh sea water) or closed (reuse of seawater).

The open seawater system has many advantages but is limited to boat use during transport. A closed, recirculated water system is used in nonboat transport situations to and from the research facility. Water is generally pumped through filters via small battery operated bilge pumps to remove any suspended particulates and solid wastes (Fig 5). An additional bilge pump, or other current producing

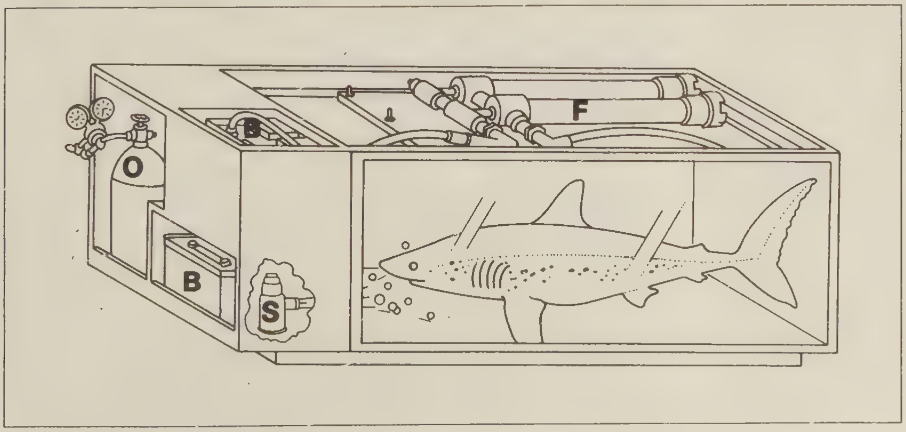

Figure 5.
Small shark transport unit. F = Filtration, O = Oxygen, B = Batteries, S = Submersible bilge pump.

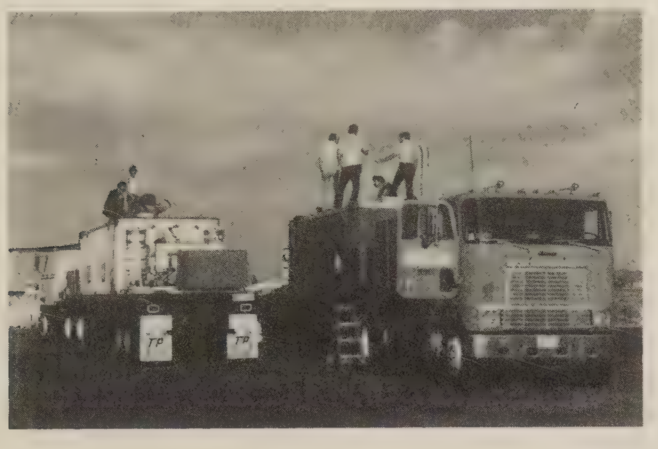

Figure 6.
This large transport unit contains the same elements as the small unit but allows free movement of both large and small fish within. The unit holds approximately 11,355 liters.

Table 1.
The composition of shark Ringer's solution, modified to counteract the effects of acidosus in shark transport.

Sodium	280 mEq/L
Potassium	4.4 mEq/L
Chloride	230 mEq/L
Urea	300 mEq/L
Dextrose	2%
pH ($NaCO_3$)	8.4

device, provides the necessary flow of water through the mouth and over the gills of the larger sharks which may require a forced flow to provide adequate respiratory exchange. A small stream of oxygen may also be passed along with this current creating a highly oxygenated environment. It has been shown that elevated O_2 levels have a mild tranquilizing effect on most elasmobranchs (Gruber and Keys 1981), which is quite desirable in a transport situation. This effect is also rapidly reversible by discontinuing the flow of O_2.

The use of anesthetics or tranquilizers during transport has been attempted by many investigators with varying results (Gilbert and Wood 1957; Clark 1963b). The disadvantage experienced in their use is not during transport but upon arrival at the facility. The use of these drugs must be carefully timed. Unless the drug is rapidly reversible, the fish may continually bump the walls of the enclosure causing damage to its sensitive eyes and snout. Severe bruising and death may result.

Water quality is critical and may be responsible for the loss of more animals during transport than any other factor. Waste products are continuously being produced and transferred to the water, primarily in the form of ammonia (NH_4^+) (Hoar and Randall 1969). Ammonia (NH_4^+), along with its by-product of nitrification, nitrite (NO_2^-), is extremely toxic and must be removed or kept at reduced levels (Spotte 1973, 1979). Generally, in an aquarium system, this would be accomplished by the use of a biological filter in which NH_4^+ is reduced to NO_2^- by nitrifying bacteria (*Nitrosomonas* sp.) and again from nitrite to relatively nontoxic nitrate (NO_3) by a second type of nitrifying bacteria (*Nitrobacter* sp.) (Spotte 1973; Smart 1978). Biological filtration is important in long transports but must be dealt with and monitored differently from the normal aquarium situation where the ratio of water volume to fish weight is generally greater. During a transport, excess water volume and weight may be a problem depending on which form of transport container is in use (Figs. 5,6). Low water volume results in a relatively high concentration of wastes, and a highly active biological filter is necessary. This type of filter may take the form of paper cartridge filters or a separate packed media filter. In either case, they must be carefully prepared prior to being put into use. Spotte (1973, 1979) presents a complete discussion of biological filter start-up procedures and filter types.

Water pH also plays a vital role in transports and must be maintained. From our experience, we suggest that pH values of 7.0 to 8.4 are acceptable with 7.8 to 8.2 being the most desirable range for elasmobranchs. The process of highly active biological filtration, respiration, and production of waste products all serve to rapidly reduce pH levels during transport. NH_4^+ becomes less soluble at a lower pH. As the pH declines, so does the toxicity of ammonia which, to a point, is a desirable effect.

The animal in transport is usually under stress which may manifest itself in an acidemic condition (acidosis) and must be controlled or counteracted. Because elasmobranchs are hyperosmotic to their environment (50–100 mOsm/liter), exposure to an elevated environmental ammonia level in itself may produce acidosis (Sousa and Meade 1977). Decreases in blood pH as a result of acidosis may be controlled to a degree by manipulation of the water pH upwards to as high as 8.4. The addition of inorganic carbonate compounds in the form of sodium bicarbonate ($NaHCO_3$) or sodium carbonate (Na_2CO_3) or organic buffers, such as tris (2-amino -2(hydroxymethyl) -1,3-propanediol), have been used successfully for control of water pH during transport. Additional monitoring of blood CO_2 levels and subsequent infusion of shark Ringer's solution (Table 1) with 2% dextrose has also proven very helpful in the counteraction of the effects of acidosis. Fluids, such as the modified Ringer's solution in Table 1, may be dripped intravenously or administered in large doses of 500 to 1000 mL intraperitoneally. Intravenous injection is most easily accomplished via the caudal vein or the dorsal vein located medially at the posterior insertion of the first or second dorsal fins. Blood samples may also be taken from these same areas. This procedure is not indicated in all transports and is generally used only with the larger species such as bull sharks, *Carcharhinus leucas*, sandbar sharks, *C. plumbeus*, and dusky sharks, *C. obscurus*—in transports lasting in excess of 10–12 hours.

A significant improvement in specimen survival has resulted from the "staging" of the animals prior to transport. The staging area is a facility into which the specimens are transferred to recover from the stress of capture. Success rates increase dramatically with the addition of this step. This staging also allows the aquarist and researcher further evaluation of specimens prior to transport. The temporary staging facility itself may consist of fiberglass or of typical above-ground swimming pool construction which is relatively inexpensive, portable and reusable. It may be designed as either an open or closed system. However, as most of these facilities are set up along the coast, the open system is usually more practical.

Facility Design and Construction

The successful maintenance of any animal must take into consideration the environmental and physiological requirements of the species. Large pelagic sharks require large facilities. Size alone, however, does not guarantee success. Over the years, a number of tank designs have been used, including donut-shaped, round or oval, and the standard rectangular design. An angle of 90° or less within a shark enclosure is simply dead space to a swimming shark of any size. Navigation of blind corners becomes difficult and probably unnatural for all but a few reef species and an energy burden because it requires considerable effort to recover from a corner.

From an economic standpoint these corners can be eliminated, thus reducing water volume or allowing redistribution of that useless volume to other areas. The larger the system volume, the greater the filtration requirements and the greater the cost of construction. Cost generally dictates size. Figure 7 shows a basic pool design which has been used successfully by several facilities and which has been described in detail by Keyes (1979).

The traditional round or donut shapes have been successful only for some species. These designs seem to be most effective for the larger sharks only when approaching volumes in excess 1.5×10^6 liters. Below this volume navigation becomes difficult, perhaps owing to the incomplete ability to perform normal and efficient swimming behaviors (Klay 1977). Large sharks repeatedly orient to the walls and predominately circle in one direction only, occasionally venturing into the center of the pool. As a rule, size and surface area play an important role and horizontal swimming space appears more important than vertical space.

Gruber and Keyes (1981) observed a definite decrease in food consumption with an increase in swimming space. It appears that a notable decrease in food consumption also occurs as energy expenditure is reduced with improved facility design. These factors also influence growth and longevity of captive sharks.

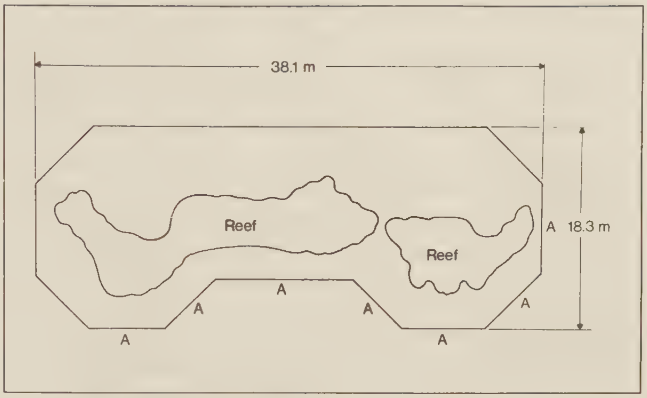

Figure 7.
Schematic shows a successful pool design. A = viewing windows. Depth varies from 3.0–5.0 m. Note the absence of blind corners. (After Weihs et al. 1981.)

Care and Maintenance

The condition in which a shark, skate or ray arrives at a facility may determine how difficult it will be to acclimate the specimen to its new environment. There are several initial concerns which must be addressed quickly. Physical health from a clinical perspective may be first. Serious abrasions, punctures, or lacerations from the capture or transport process should be evaluated and may require attention in the form of topical or antibacterial treatment. Parasitic infestations must be eliminated. Most specimens have some type of external trematode, copepod, or leech which, in an aquarium environment, may be detrimental to the longterm health of the animal. Monogenetic trematodes in particular may pose a life threatening problem if left unchecked. Many parasite species have developed a host specificity and are a common problem in sharks (Gruber and Keyes 1981; Cheung et al. 1982; Cheung and Ruggieri 1983; Cheung and Nigrelli 1983; Goven and Amend 1982). Treatments for control or elimination of the parasites vary. Table 2 indicates several treatments used most commonly. Treatment effectiveness also varies and may be influenced by the species, dosage of drugs or chemicals, water quality, temperature and pH (Bylund and Sumari 1981; Schmahl and Mehlhorn 1985).

An elasmobranch in good health and under relatively low levels of stress should eat soon after acclimation. The effects of fasting in sharks has been described in detail by Martini (1978), Gruber and Keyes (1981), and Baldridge (1972) and should not be allowed to persist beyond three to four weeks. In those instances in which a specimen is

Table 2.
Drugs and chemicals used in The treatment of parasitic diseases of elasmobranchs.

Drug/chemical	Manufacturer	Dosage
Trichlorfon	AquaVet Haywood, CA	0.4 to 2.0 ppm in water 6–8 h duration
Copper sulfate		.05 to .20 ppm in water 6–8 wk duration
Droncit (Praziquantel)	Mobay Corp. Shawnee, KS	20 mg/L in water (56.8 mg/mL injectable) 24 h duration
Ivermectin	Merck and Co. Rahway, NJ	200 μg/kg IM.

reluctant to eat it may be necessary to intervene. A clinical workup including hematology, serum chemistries, and microbiology may point to a problem which may be treatable.

The decision to treat for inappetence should depend on a number of other factors as well, including the normal acclimation time for each species, the animal's attitude and activity, and its clinical appearance and weight.

Initial therapy may include the parenteral administration of appetite stimulants such as Vitamin B-complex (1 cc/12 kg body weight) or steroids such as Winstrol (1 mg/10 kg BW) or Flucort (.5 mg/10 kg BW). These have been used with success; however, since the full effects of steroids on shark physiology are presently not known, the use of these compounds should be approached with caution.

Force feeding has been successful in really stubborn cases and should be initiated prior to any severe weight loss.

Information about elasmobranch dietary supplementation is inadequate compared with cultured bony fish and other aquatic animals (Halver 1972; Cowey et al. 1985; Jackson and Cooper 1981). Table 3 lists a broad supplementation which has been in use at Sea World of Florida for the past eight years with apparently good results. Much work, however, remains in the area of nutrition. As we keep these animals for longer periods, diet-related abnormalities and disease will become apparent.

Many large oceanaria and aquaria have established clinical veterinary programs specifically designed for elasmobranchs. Baseline information from captive animals which allows physiological assessment of their condition is growing at an increasing rate; and "normal" values from free-ranging sharks, skates, and rays are being added to data bases for comparison. (Walsh and Murru 1984; Murru and Case 1984; Stoskopf et al. 1986). This new information in combination with continued advances in equipment and facility design will continue to improve our ability to keep and study in detail these highly specialized animals.

Table 3.
Elasmobranch vitamin and mineral supplement supplied once/week with minimum food. Elasmobranchs less than 60 kg received multiple vitamin, potassium iodide, and kelp only.

Potassium iodide	15.0	mg/kg
Kelp	.005	mg/kg
Vitamin A	833.3	IU/kg
Vitamin E	6.7	IU/kg
Vitamin C	33.3	mg/kg
Vitamin B_1	5.0	mg/kg
Ferrous gluconate	83.3	mg/kg
Bone meal	.003	mg/kg
Multiple vitamin (containing)		
A	12,500	IU
D_3	2,500	IU
E	31.2	IU
C	125	mg
B_1	6.5	mg
B_2	6.5	mg
B_6	3.75	mg
B_{12}	15	mcg
Niacin	10	mg
Pantothenic acid	9.2	mg
Iron	25	mg
Choline		trace
Inositol		trace
Folic acid		trace
Kelp		trace

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Reproduction of Elasmobranchs in Captivity

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ABSTRACT

Observations of reproductive behavior of elasmobranchs are rarely made and not usually reported in the scientific literature. Owing to exceptionally good conditions for maintaining elasmobranchs at the Okinawa Expo Aquarium, Japan, reproduction in several species has been observed in detail. From May 1975 to July 1987, 40 species of 12 families of sharks and 16 species of 5 families of rays were kept in captivity. Reproduction in seven species of sharks and seven species of rays was observed and is reported here. The species of sharks observed were *Heterodontus japonicus*, *Orectolobus japonicus*, *Stegostoma fasciatum*, *Scyliorhinus torazame*, *Cephaloscyllium umbratile*, *Triaenodon obesus*, and *Carcharhinus plumbeus*. The species of rays observed were *Dasyatis ushiei*, *Dasyatis sephen*, *Himantura uarnak*, *Aetobatus narinari*, *Rhinoptera javanica*, *Rhynchobatus djiddensis*, and *Rhina ancylostoma*. Fertilization occurred in captivity in *S. torazame*, *C. plumbeus*, *T. obesus*, *A. narinari*, and *R. ancylostoma*. Breeding behavior was observed in the aquarium as follows: mating behavior in four species: *S. torazame*, *T. obesus*, *A. narinari*, and *R. javanica*; birth in four species: *T. obesus*, *C. plumbeus*, *A. narinari*, and *R. djiddensis*; and egg-laying in three species: *S. torazame*, *S. fasciatum*, and *H. japonicus*. Tank-born mothers of *S. torazame* and *T. obesus* gave birth to a second generation in captivity. Breeding seasons, gestation periods and data on newborn elasmobranchs are reported.

Elasmobranchs Bred in Captivity in the World

According to "The species bred in captivity" published in the International Zoo Yearbooks (1963–1986), 25 species in six families of sharks and 18 species in eight families of rays were bred in captivity from 1962 to 1983 (Tables 1, 2). The yearbooks list species bred in captivity, meaning those born or hatched in aquaria, marine life parks, and other man-made facilities as the result of matings in captivity. Species listed in the yearbook with comments of noncaptive fertilization, and species from Japanese aquaria which were ascertained by personal communication to be, in fact, gravid at capture, have been excluded from Tables 1 and 2. If detailed inquiries were made on all the species in the Yearbook lists, it is likely that further instances of errors in reporting (that is, fish captured in a fertilized condition) would be found. Big tanks, where large and fast-swimming sharks and rays can be kept, were not built until the 1970's. Consequently, most elasmobranchs bred in captivity in the past were small and sluggish species. Owing to the recent use of huge tanks, some comparatively large, pelagic, and fast-swimming elasmobranchs (such as species of Carcharhinidae and Myliobatididae) have been kept and bred successfully in captivity. However, species of Alopiidae, Lamnidae, larger species of Sphrynidae, Mobulidae, and most deep-sea species of elasmobranchs are difficult to maintain for long periods of time, and consequently their successful reproduction in captivity has yet to be accomplished.

Elasmobranchs Born or Hatched[1] in Captivity in Japan

Records of elasmobranchs born or hatched in captivity at aquaria in Japan are shown in Tables 3 and 4. They are summarized from written questionnaires compiled by Ueno Zoo Aquarium (1983) and telephone surveys made by Okinawa Expo Aquarium (1987). At aquaria in Japan, 17 species in eight families of sharks and 19 species in eight families of rays were born or hatched in captivity from 1977 to 1987. Among them, seven species of sharks and three species of rays were bred as a result of captive fertilization. Only these ten species merit being included in the previously mentioned lists published in the International

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[1] The words "born or hatched" as used here mean "bred in captivity," that is, born or hatched either as a result of mating in tanks or as a result of mating in the wild.

Table 1.
Sharks bred in captivity in the world, 1962–1983.[a]

Family	Species	Place and no. of aquaria
Heterodontidae	*Heterodontus francisci*	USA 2
	H. japonicus	JAP 1
	H. mexicanus	USA 1
Scyliorhinidae	*Cephaloscyllium umbratile*	JAP 1
	C. uter	USA 1
	C. ventriosum	USA 2
	Scyliorhinus canicula	EUR 18
	S. stellaris	EUR 6
	S. torazame	JAP 8
	Scyliorhinus sp.	EUR 1
	Apristurus brunneus	USA 1
Triakididae	*Mustelus californicus*	USA 1
	M. norrisi	USA 1
	Triakis scyllia	JAP 2
	T. semifasciata	USA 1
Carcharhinidae	*Triaenodon obesus*	JAP 1
	Carcharhinus leucas	USA 1
	C. plumbeus	JAP 1
Sphyrnidae	*Sphyrna tiburo*	USA 1
Orectolobidae	*Orectolobus japonicus*	JAP 1
	Ginglymostoma cirratum	EUR 1, USA 1
	Chiloscyllium griseum	EUR 1
	C. indicum	ASIA 1
	Hemiscyllium hallstromi	AUSTRAL 1
	Hemiscyllium sp.	EUR 2

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[a] Data from International Zoo Yearbooks, 1963–1986 (Vols. 3 to 24/25), Zool. Soc. London.

Zoo Yearbooks. Species of elasmobranchs that were born or hatched after fertilization in captivity are few compared with those that were fertilized before being captured, i.e., 41% (seven species) of the total shark species and only 16% of the total ray species were born or hatched in captivity in Japanese aquaria. Births and hatchouts are few, both in number of aquaria with occurrences and in number of occurrences. An exception in sharks is the frequency of reproduction of *Scyliorhinus torazame*, in both number of aquaria and number of occurrences. An exception in rays is that of *Aetobatus narinari*, which reproduced in captivity many times, although at only one aquarium.

Environment for Elasmobranchs at Okinawa Expo Aquarium

Environmental data for elasmobranchs kept in captivity at Okinawa Expo Aquarium (OEA) are shown in Table 5. The water for the Deep Sea tank is artificially cooled to a temperature of 11.3°C., with a minimum of 9.1°C and a maximum of 13.7°C. The water in the Coral Sea tank and the Kuroshio tank is neither cooled nor heated, with the exception of being heated from 22°C to 24.5°C during one winter when a whale shark was maintained. Seasonal changes in water temperature differ by only 0.1°C. between the Coral Sea and Kuroshio tanks.

Table 2.
Rays bred in captivity in the world, 1962–1983.[a]

Family	Species	Place and no. of aquaria
Torpedinidae	*Torpedo marmorata*	EUR 2
	T. ocellata	EUR 1
Rhinobatidae	*Rhina ancylostoma*	JAP 1
	Rhinobatos productus	USA 1
Rajidae	*Raja binoculata*	USA 1
	R. clavata	EUR 1
	R. texana	USA 1
	R. undulata	EUR 1
Urolophidae	*Urolophus jamaicensis*	USA 3
Dasyatididae	*Dasyatis americana*	USA 2
	D. matsubarai	JAP 1
	D. pastinaca	EUR 1
	D. sabina	USA 1
Gymnuridae	*Gymnura micrura*	USA 1
Myliobatididae	*Myliobatis californicus*	USA 1
	Aetobatus narinari	JAP 1, USA 1
Potamotrygonidae	*Potamotrygon motoro*	EUR 1, USA 1
	Potamotrygon sp.	EUR 1

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[a] Data from International Zoo Yearbooks, 1963–1986 (Vols. 3 to 24/25), Zool. Soc. London.

Elasmobranchs Kept in Captivity at OEA

During 12 years and 3 months, from May 1975 to July 1987, 56 species of elasmobranchs were kept in captivity at Okinawa Expo Aquarium. These consisted of 40 species in 12 families of sharks and 16 species in five families of rays (Tables 6, 7). Sharks in the families Scyliorhinidae and Squalidae, and *Heptranchias perlo*, *Cirrhoscyllium expolitum*, and *Squatina nebulosa*, were kept in the Deep Sea tank. *Heterodontus japonicus*, *Orectolobus japonicus*, *Nebrius concolor*, and *Triaenodon obesus* (tank-born individuals), were kept in the Coral Sea tank. Species of Carcharhinidae and Triakiidae, and *Rhincodon typus*, *Alopias pelagicus*, *Isurus oxyrinchus*, and *Sphyrna lewini* were kept in the Kuroshio tank. Twenty species of sharks (50% of the total) and ten species of rays (63%) survived for over six months. The longest periods of captivity for 26 species are reported in Table 8.

Table 3.
Sharks born or hatched in captivity in Japan, 1977–1987. HCA = Hameji City Aq.; HYP = Hiyoriyama Park; IMP = Inubosaki Marine Park; KSW = Kamogawa Sea World; MSA = Matusima Aq.; MSM = Marine Science Museum of Tokai Univ.; MSP = Mito Sea Paradise; NGA = Niigata Aq.; NSA = Nagasaki Aq.; OAA = Ooarai Aq.; OEA = Okinawa Expo Aq.; OGA = Oga Aq.; OTA = Oita Ecological Aq.; SAK = Shirahama Aq. of Kyoto Univ.; SFA = Shimoda Floating Aq.; SMM = Shima Marineland; TBA = Toba Aq.; TDA = Teradomari Aq.; TSA = Takesima Aq.; TWM = Taiji Whales Museum; UZA = Ueno Zoo Aq.; YSP = Yasima Sea Palace.

		Occurrence of birth or hatching by fertilizing condition		
Family	Species	In aquaria	Before capture	Unknown
Heterodontidae	*Heterodontus japonicus*	[a]1/1 (SFA)	3/6 (OEA3, TWM, TSA2)	2/3 (MSM, SFA2)
Scyliorhinidae	*Cephaloscyllium umbratile*	1/1 (SFA)	6/6 (IMP, KSW, MSP, OEA, SAK, YSP)	1/2 (SFA2)
	Scyliorhinus torazame	8/33 + (KSW8, MSA, OAA2, OEA12 +, OGA, SFA4, TDA4, UZA +)	2 + /5 + (IMP2 +, OAA3, etc.)	
	Scyliorhinius sp.			1/1 (SFA)
	Parmaturus pilosus		1/1 (SMM)	1/1 (SFA)
	Halaelurus buergeri		1/1 (NSA)	
Triakididae	*Mustelus manazo*		3/3 (IMP, MSA, TWM)	1/1 (TBA)
	M. griseus		2/2 (HCA, TWM)	
	Triakis scyllia	2/2 (SFA, TBA)	6/8 (HCA, NGA, MSP, OAA, SFA3, TWM)	2/3 (HYP, TBA2)
	Proscyllium venustum		1/1 (YSP)	
Carcharhinidae	*Triaenodon obesus*	1/5 (OEA5)	1/2 (OEA2)	
	Carcharhinus plumbeus	1/2 (OEA2)	1/1 (OEA)	
Orectolobidae	*Orectolobus japonicus*	1/1 (OTA)	2/5 (OEA2, SFA3)	
	Stegostoma fasciatum		1/1 (OEA)	
Squalidae	*Etmopterus lucifer*	2/2 (IMP, TWM)		
Pristiophoridae	*Pristiophorus japonicus*		1/1 (TWM)	
Squatinidae	*Squatina japonica*		5/5 (HCA, IMP, NSA, OAA, TWM)	

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[a] Number of aquaria/number of occurrences.

Table 4.
Rays born or hatched in captivity in Japan, 1977–1987. HCA = Hameji City Aq.; IMP = Inubosaki Marine Park; KAM = Keikyu Aburatsubo Marine Park Aq.; KMP = Kusimoto Marine Park; MCB = Minamichita Beahland; MSA = Matusima Aq.; NSA = Nagasaki Aq.; NWS = Nanki Shirahama Workd Safari; OEA = Okinawa Expo Aq.; SAK = Shirahama Aq. of Kyoto Univ.; SFA = Shimoda Floating Aq.; SIA = Sunshine International Aq.; TSA = Takesima Aq.; UZA = Ueno Zoo Aq.

		Occurrence of birth or hatching by fertilizing condition	
Family	Species	In aquaria	Before capture
Torpedinidae	*Narke japonica*		4/4 (MSA, SFA, TSA, TWN)
Rhinobatidae	*Rhina ancylostoma*	[a]1/1 (OEA)	
	Rhynchobatus djiddensis		1/2 (OEA2)
	Rhinobatos hynnicephalus		2/2 (NSA, SAK)
	R. schlegelii		3/3 (NWS, SAK, TSA)
Platyrhinidae	*Platyrhina sinensis*		4/4 (MTB, NSA, SAK, SFA)
Rajidae	*Raja kenojei*		3/4 (IMP2, KMP, NSA)
	R. acutispina		1/1 (KMP)
	R. porosa		1/1 (MSA)
Urolophidae	*Urolophus aurantiacus*	1/1 (HCA)	
Dasyatididae	*Dasyatis sephen*		1/1 (OEA)
	D. violacea		1/1 (KAM)
	D. matubarai	1/1 (KAM)	
	D. ushiei		1/1 (OEA)
	D. akajei		4/4 (HCA, MSA, SIA)
	Dasyatis sp.		1/1 (SFA)
	Himantura uarnak		1/3 (OEA3)
Myliobatididae	*Aetobatus narinari*	1/9 (OEA9)	
Rhinopteridae	*Rhinoptera javanica*		1/3 + (OEA3 +)

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[a] Number of aquaria/number of occurrences.

Table 5.
Environmental data for elasmobranchs at the Okinawa Expo Aquarium.

A) Tanks for keeping elasmobranchs

Name	Length	Width	Depth (m)	Capacity (t)	Water turnover rate (turnover/day)		
					Filtered	New seawater	Total
Kuroshio	27	12	3.5	1,100	10	7	17
Coral Sea	12	12	2.1	200	15	8	23
Deep sea							
A	3.7	2	2.4	15	17	2	19
B	1.2	1	0.8	0.8	17	2	19

B) Water parameters of tanks

Name	Water temperature (°C)			pH			Salinity ($^0/_{00}$)		
	Minimum	Maximum	Average	Minimum	Maximum	Average	Minimum	Maximum	Average
Kuroshio	19.8	29.6	24.6	7.9	8.35	8.2	33.04	37.36	35.79
Coral Sea	19.8	30.2	24.7	8.1	8.40	8.3	32.25	37.00	35.77
Deep sea	9.1	13.7	11.3	7.7	8.40	8.2	34.08	36.23	35.62
Seawater[a]	19.8	30.1	24.4	8.3	8.40	8.4	34.43	36.44	35.74

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[a] Seawater temperature measured immediately after the first gravity sand filter.

Table 6.
Sharks kept in captivity at the Okinawa Expo Aquarium, May 1975–July 1987.

Family	Species
Heterodontidae	*Heterodontus japonicus*
Hexanchidae	*Heptranchias perlo*
Scyliorhinidae	[a]*Cephaloscyllium umbratile*
	[a]*Scyliorhinus torazame*
	[a]*Scyliorhinus* sp.
	Galeus eastmani
	G. sauteri
	Parmaturus pilosus
	Halaelurus buergeri
Triakididae	[a]*Mustelus manazo*
	[a]*M. griseus*
	[a]*Triakis scyllia*
	[a]*Proscyllium venustum*
	[a]*Hemitriakis japanica*
Orectolobidae	[a]*Orectolobus japonicus*
	Cirrhoscyllium expolitum
	[a]*Stegostoma fasciatum*
	[a]*Nebrius concolor*
Rhincodontidae	[a]*Rhincodon typus*
Alopiidae	*Alopias pelagicus*
Lamnidae	*Isurus oxyrinchus*
Carcharhinidae	[a]*Galeocerdo cuvier*
	[a]*Triaenodon obesus*
	Prionace glauca
	[a]*Carcharhinus altimus*
	C. falciformis
	[a]*C. Leucas*
	[a]*C. longimanus*
	C. melanopterus
	[a]*C. obscurus*
	[a]*C. plumbeus*
Sphyrnidae	*Sphyrna lewini*
Squalidae	*Etmopterus lucifer*
	Squalus mitsukurii
	S. brevirostris
	Squalus sp.
	Centrophorus atromarginatus
	C. scalpratus
	Squaliolus alii
Squatinidae	[a]*Squatina nebulosa*

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[a] Species kept for over six months.

Table 7.
Rays kept in captivity at the Okinawa Expo Aquarium, May 1975–July 1987.

Family	Species	Family	Species
Dasyatididae	[a] *Dasyatis sephen*	Rhinopteridae	[a] *Rhinoptera javanica*
	[a] *D. ushiei*	Mobulidae	*Mobula japanica*
	D. kuhlii		*M. diabolus*
	[a] *D. akajei*		*M. formosana*
	[a] *Himantura uarnak*		*Manta birostris*
	[a] *Himantura* sp.	Rhinobatidae	[a] *Rina ancylostoma*
	Taeniura melanospila		[a] *Rhynchobatus djiddensis*
Myliobatididae	[a] *Aetobatus narinari*		[a] *Rhinobatos schlegelii*

[a] Species kept for over six months.

Table 8.
The longest survival time of 29 elasmobranch species kept in the Okinawa Expo Aquarium as of July 1987.

Sharks			Rays	
Species	Time (yr/m)	Remarks	Species	Time (yr/m)
Heterodontus japonicus	2/0		*Rhina ancylostoma*	6/11
Scyliorhinus torazame	12/3 +		*Rhynchobatus djiddensis*	5/1
Galeocerdo cuvier	1/9		*Dasyatis sephen*	0/8
Triaenodon obesus	10/1	Tank born individual	*D. ushiei*	8/6 +
Carcharhinus longimanus	0/7	Eaten by *Carcharhinus leucas*	*Himantura uarnak*	11/1 +
C. plumbeus	7/11 +		*Himantura* sp.	8/6
C. obscurus	4/4 +		*Mobula japanica*	7 days
C. leucas	9/1 +		*M. diabolus*	1 day
C. altimus	5/4	Eaten by *Carcharhinus leucas*	*M. formosana*	1 day
Prionace glauca	30 days		*Manta birostris*	4 days
Sphyrna lewini	48 days	Eaten by *Carcharhinus leucas*	*Aetobatus narinari*	11/0 +
Alopias pelagicus	1 day	Eaten by *Carcharhinus altimus* and *C. leucas*	*Rhinoptera javanica*	12/0 +
Stegostoma fasciatum	8/4 +			
Nebrius concolor	7/8 +			
Rhincodon typus	1/9			
Isurus oxyrinchus	1 day			
Squatina nebulosa	0/8			

Reproduction of Elasmobranchs in Captivity at OEA

Reproduction Records

Birth or hatching in seven species of sharks and seven species of rays was observed from 1975 to 1987 in fish tanks at the OEA (Tables 9, 10). Among the sharks which reproduced, mating behavior was observed in two (*Scyliorhinus torazame*, *Triaenodon obesus*) (Table 11) and although not observed, certainly occurred in the tank for one (*Carcharhinus plumbeus*). The gravid females of the four other species (*Heterodontus japonicus*, *Cephaloscyllium umbratile*, *Orectolobus japonicus*, and *Stegostoma fasciatum*) were pregnant when captured. Successful hatching occurred in all species except *Stegostoma fasciatum*. A gravid female of this species laid six large eggs after capture and was transferred to the aquarium, but the eggs did not hatch (Fig. 1). Among the rays, mating was observed in two species: *Aetobatus narinari* and *Rhinoptera javanica* (Table 11). Fertilization was confirmed for *R. ancylostoma* (one case, Fig. 2) and *A. narinari* (nine cases, for a total of 16 offspring born from one mother from 1977 to 1986). There is a high probability of fertilization in captivity of *Rhinoptera javanica* because copulations in this species have been observed many times in the Kuroshio tank; however, because so many rays of this species are kept in the tank (about 50 including adults and tank-born pups), individual identification was difficult. Whether fertilization of gravid females took place in the sea or in our tank could not be determined for female *Rhinoptera*

Table 9.

Data on birth or hatching of sharks at the Okinawa Expo Aquarium, May 1975–August 1987. Figures in parentheses show number of young born as the result of mating in captivity. TL = Total length; BW = Body weight; Sex ratio = Number of male/number of female.

	Mother					Sex ratio	
Species	*N*	TL (cm)	BW (kg)	Number per liter	Total number born or hatched	*N*	Ratio
Heterodontus japonicus	1	110	10	1–2	11	10	1.0
Scyliorhinus torazame	3	44–50	0.53–0.63	1–2	234(234)		
Cephaloscyllium umbratile	1	100	7.5	1–2	1		
Triaenodon obesus	5	ca. 135–160	ca. 8–20	1–3	10(8)	11	2.33
Carcharhinus plumbeus	3	185–190	46–ca. 60	6–10	33(14)	32	1.91
Orectolobus japonicus	2	100–107	7.0–7.5	1–?[a]	32	32	0.68
Stegostoma fasciatum	1	223	45	1–3	6 (Eggs laid out, not hatched)		

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[a] Not exactly confirmed.

Table 10.

Data on birth or hatching of rays at the Okinawa Expo Aquarium, May 1975–July 1987. Figures in parentheses show number of young born as the result of mating in captivity. DW = Disk width; BW = Body weight; TL = Total length.

	Mother					Sex ratio	
Species	*N*	DW (cm) or TL	BW (kg)	Number per liter	Total number born	*N*	Ratio
Rhina ancylostoma	1	224 TL	110	4	4(4)	4	0.33
Rhynchobatus djiddensis	2	270–272 TL	97–125.5	6–8	14	14	1.00
Dasyatis ushiei	2	127–ca. 220	59.5–ca. 200	1–4	5	4	3.00
D. sephen	1	149	81	2	2[a]	2	2 M
Himantura uarnak	1	145	53	1–2	5	4	1.00
Aetobatus narinari	1	ca. 140	ca. 60	1–2	16(16)	10	1.50
Rhinoptera javanica	1	96	15	1	17[b]	—	—

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[a] Stillbirth.

[b] Not exactly confirmed.

Table 11.

Data on the mating of elasmobranchs observed at the Okinawa Expo Aquarium.

Species	Date	Copulation period	Clasper used
Scyliorhinus torazame	11 April 1981	4 min	Left
	4 June 1981	—	Right
Triaenodon obesus	22 June 1980	15 s–3 min	Right
	11 August 1987	1.5 min	Left
Aetobatus narinari	3 September 1979	0.5–1.5 min	Left?
Rhinoptera javanica	23 August 1978	—	Left
	23 June 1981	—	Both
	2 July 1981	33 s	?
	14 June 1982	30 s	Right
	14 June 1982	20 s	?
	14 June 1982	35 s	Left

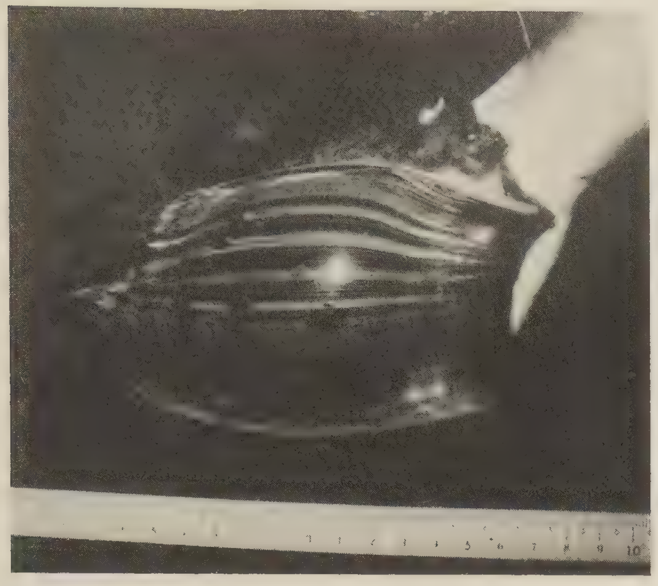

Figure 1.
One of six egg cases laid by *Stegostoma fasciatum*, 4 May 1985. Length 17.0 to 18.0 cm; width 9.5 to 10.5 cm; thickness 3.7 to 5.0 cm. None of these cases hatched.

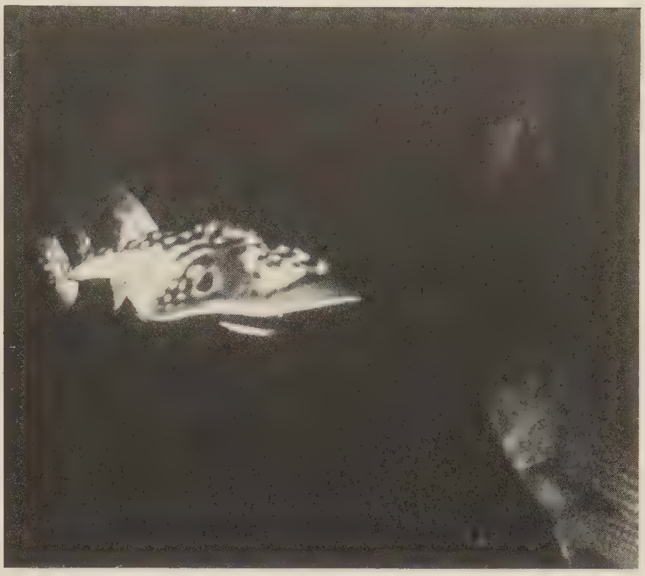

Figure 2.
Newborn pup of *Rhina ancylostoma*, Kuroshio tank, 10 November 1986. Four pups were born, surviving 3 days.

(Tables 10, 12). Females of the other four species were known to be gravid when captured. Survival periods and numbers of newborn or newly hatched elasmobranchs are shown in Tables 12 and 13. To date, survival has been higher in sharks than in rays. As of July 1987, we kept in captivity 123 individuals of five species of tank-born sharks, compared to nine individuals of only one species of ray. Moreover, these nine individuals of *R. javanica* may not be an accurate number, as explained above. The best breeding success in the Okinawa Expo Aquarium was shown by three species of sharks, *S. torazame*, *T. obesus*, and *C. plumbeus*. This success suggests a high adaptability to a captive environment, and, especially, to the facilities and environmental conditions we provided. In rays, *A. narinari* and *R. javanica* produced relatively good results. We were able to observe their mating and birth behavior many times, and we obtained much information on their reproduction. We were not, however, able to keep their young alive for long periods of time.

Observations on Mating

Observation of mating behavior was made on two species of sharks, *S. torazame* and *T. obesus*, and two species of rays, *A. narinari* and *R. javanica* (Table 11). In these four species, one clasper (left or right) was used for insertion, except on one occasion when a male *R. javanica* inserted two claspers simultaneously. Copulating posture was abdomen to abdomen, with the female lying on her back on the bottom of the tank. Durations of insertions were from 15 s to 4 min in both species of sharks, and from 20 s to 1 m in both species of rays.

Scyliorhinus torazame—Mating of *S. torazame*, observed twice (Fig. 3A, B), is reported in the Discussion section.

Triaenodon obesus—On 27 June 1983, two six-year-old tank-born *T. obesus* from the same litter copulated with each other. In this copulation, the male (total length [TL] 142 cm and body weight [BW] ca. 20 kg) bit the female (TL 135 cm and BW of ca. 18 kg) on her right pectoral fin, in a side to side position. Then, the male bent his tail to the left, and bent his right clasper to the left for insertion (Fig. 4). Thirteen months after this copulation, the female gave birth to a male (see Second Generation Captive Birth). Three years after this birth, at the age of 10 years and 2 months, the same female gave birth to three young. The young were aborted; two were stillborn, and one died the following day. The birth occurred at 13:15, 11 August 1987, and at 15:20 the mother shark mated again. This time she mated with the brother of her 1983 partner. In this mating, the male at first bit the female on her right pectoral fin and swam together with her, moving a distance of about 7 m (Fig. 5A, A′). After reaching a corner of the tank with rocks, the male released her once, and then bit her again on the left pectoral fin (Fig. 5B, B′). Lying on his back on the bottom, the male inserted his left clasper at a 90 degree angle to his body axis (Fig. 5C, C′). After 1.5-min insertion he withdrew his clasper and swam away with the tip of the used left clasper spread and slightly bent for 5 to 10 min (Fig. 5D, D′).

Table 12.
Data on the survival of newborn rays born or hatched at the Okinawa Expo Aquarium, May 1975–July 1987. DW = Disk width; BW = Body weight; TL = Total length.

	Size and weight at birth				Longest period kept	Number of living young as of July 1987
Species	*N*	DW (cm) or TL	*N*	BW (g)		
Rhina ancylostoma	4	46.0–47.5 TL	4	830–920	3 days	0
Rhynchobatus djiddensis	14	43.0–54.0 TL	14	500–700	0 yr/11 mo	0
Dasyatis ushiei	4	av. 40.8	4	av. 2,200	1/7	0
D. sephen	2	21.0–21.5	2	350–370	Stillbirth	—
Himantura uarnak	3	35.0–40.0	1	1,800	0/6.5	0
Aetobatus narinari	4	50.0–59.0	7	2,000–4,000	2/3	0
Rhinoptera javanica	3	38.0–47.0	3	1,250–1,950	7/11[a]	9[a]

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[a] Not exactly identified.

Table 13.
Data on the survival of newborn sharks born or hatched at the Okinawa Expo Aquarium, 1975–1987. TL = Total length; BW = Body weight.

	Size and weight at birth				Longest period kept	Number of living young as of July 1987
Species	*N*	TL (cm)	*N*	BW (g)		
Heterodontus japonicus	6	20.0–22.5	6	65–70	1 yr/6 m +	4
Scyliorhinus torazame	13	8.0–9.5	13	2.8–3.7	11/4 +	72
Cephaloscyllium umbratile	1	—	—	—	0/1	0
Triaenodon obesus	10	59.0–69.0	10	800–2,000	10/3 +	8
Carcharhinus plumbeus	32	60.0–70.0	32	1,450–2,000	3/0 +	14
Orectolobus japonicus	23	21.0–23.2	23	50–110	1/3 +	25
Stegostoma fasciatum	6	17.0–18.0 (Length of egg case)	—	—	Not hatched	—

Aetobatus narinari—After an 11-mo gestation period, a female gave birth to two pups from 22:45 to 22:50 on 3 September 1979 in the Kuroshio tank. Immediately after birth, copulations started with males who had been chasing and nibbling her dorsal surface (typical ray premating behavior) before birth, at 21:30. This female mated with three or four males during one hour, from 23:00 to 24:00. On one occasion, a male of one-meter disk width bit the front margin of her pectoral fin and copulated in an abdomen to abdomen posture. The inserted clasper was perhaps the left one, but this was not confirmed (Fig. 6A). Duration of insertion was about 0.5 to 1.5 min, and leaking semen formed a white cloud. In another case, during a series of copulations, a male bit the rear edge of the right pectoral fin of a female and mated in the same posture as described above (Figs. 6C, 7C,D). From a photograph taken before insertion, it appeared that the right clasper was used because it was slightly bent just before insertion (Figs. 6B, 7B).

Rhinoptera javanica—On 14 June 1982, at 14:55, mating of a female by several males was observed at 2 m from the bottom of the tank in an abdomen to abdomen posture, the female above and the male below. The right clasper was inserted for about 30 s and was spread at the tip after withdrawal. Just after copulation the lower part of the abdomen of the female was swollen abnormally and she ejected semen from her cloaca, swimming horizontally and moving muscles around the cloaca for one minute. The ''ejection'' resembled a vapor trail from an airplane. The swollen part of her belly was about 5 cm in height and varied in shape during the ejection of semen.

At 15:00, this female swam restlessly with a still swollen abdomen and at 15:20 mated again. She was observed ejecting semen while swimming at 16:00. At 16:20 she mated with a male below her at the bottom of the tank for 20 s with her cephalic fin lowered down. During the 20-s insertion, 3 other males mounted on her back to nibble her dorsal surface, with their cephalic fins lowered down. At 16:30 mating occurred again at the bottom of the tank. A male bit the same female on the rear edge of her pectoral fin and inserted his left clasper for 35 s in an abdomen

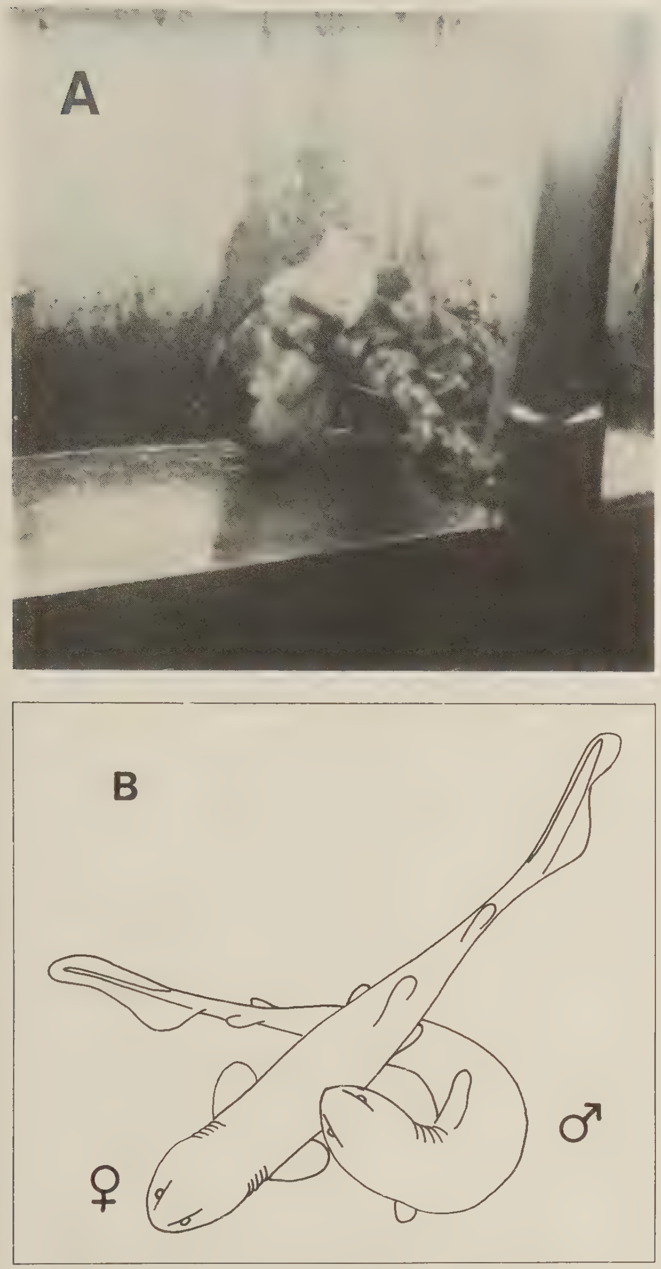


Figure 3.
Mating of *Scyliorhinus torazame*. A, Wrapping posture: male (left) inserting the right clasper; left clasper and ventral surface of pelvic fins form a white oval. (Photographed 4 June 1981.) B, Male biting female on left flank, bending his body to right and inserting the left clasper. (Observed 11 April 1981.)

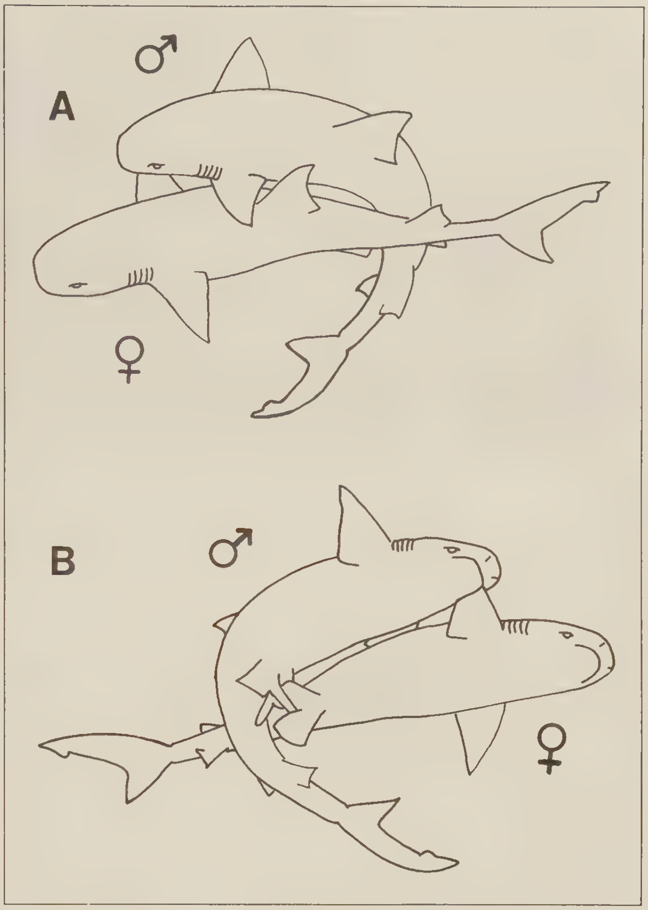


Figure 4.
Copulation of *Triaenodon obesus*, 2 June 1983. Tank-born male (6 years old) biting his litter-mate on her right pectoral fin, bending his tail to left and inserting bent-to-left right clasper. A, Dorsal view; B, Ventral view.

to abdomen position from beneath her (Fig. 8A). After the clasper was withdrawn the female stayed motionless at the bottom for a while with her cephalic fins lowered. To observers she appeared stupefied by fatigue (Fig. 8B). We were keeping about 20 males and 20 females of *R. javanica* at the time. Usually only one female at a time came into estrus. So, many males stormed the same female for mating (Fig. 8C). Almost all the individuals of this species which died in the tank were females. They died because of severe wounds on the back produced by the numerous mating bites of the males, and because of exhaustion from mating with so many males. Unlike *A. narinari* we have not observed mating behavior after birth in *R. javanica*. Mating behavior of *R. javanica*, recorded in 1979 with 8 mm movie film, consisted of a pair copulating near the surface, and dropping down together to the bottom of the tank. There they swivelled horizontally 180°, remaining in the abdomen-to-abdomen position, but now head to tail (Fig. 9A, B).

Observations on Birth

Birth of elasmobranchs was observed in four species: *T. obesus*, *C. plumbeus*, *R. djiddensis*, and *A. narinari* (Table 14). Members of Hokuto Movie Productions, Tokyo, and our aquarium staff took videos of birth and subsequent

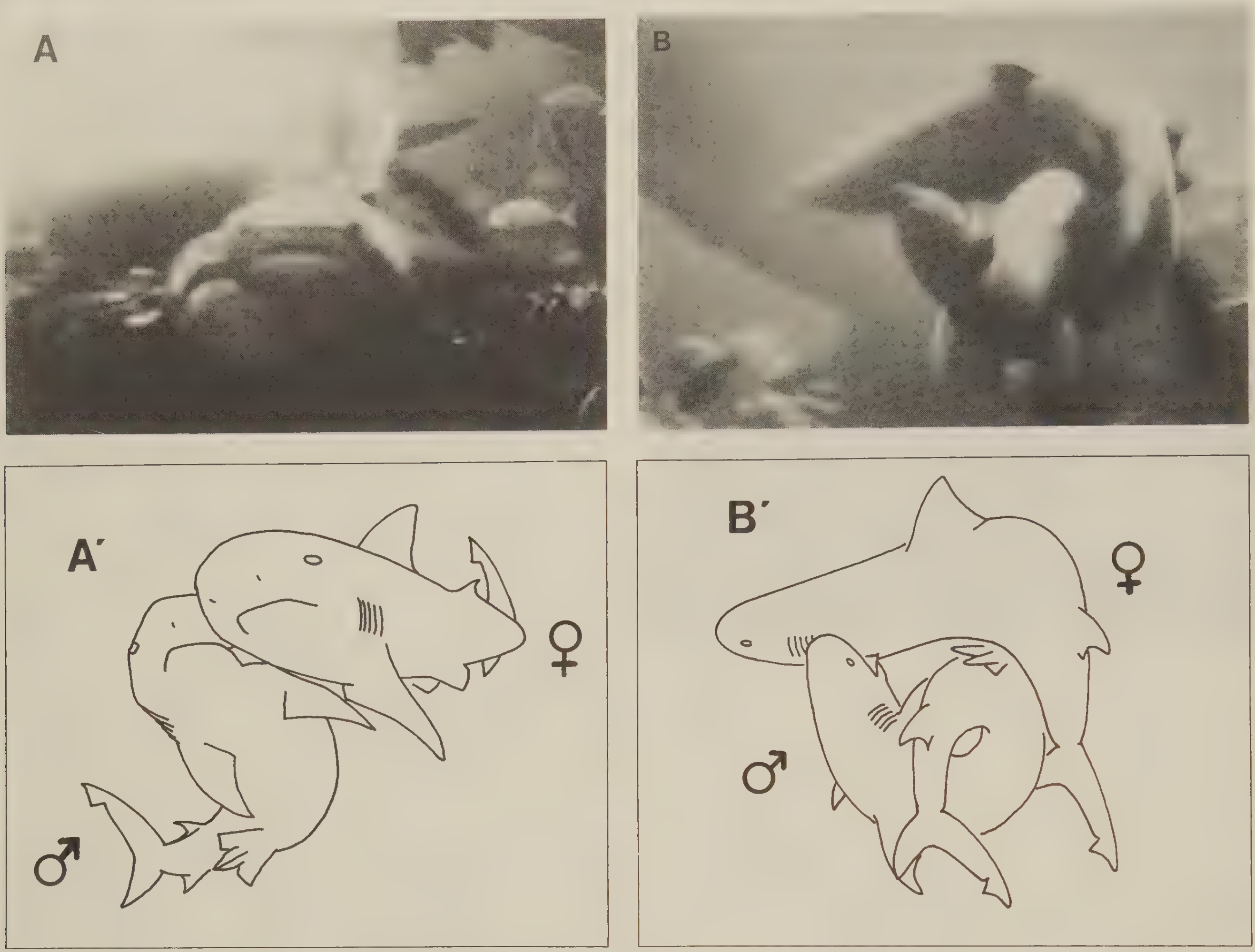


Figure 5.
Copulation of *Triaenodon obesus*, 11 August 1987. A, A′, Brother of mating male (Fig. 4) biting the same female on her right pectoral fin and swimming together with her for a distance of about 7 m. B, B′, After reaching corner of tank and releasing her, he again bites her on the left pectoral fin. Female above, male below.

behavior of newborn *C. plumbeus* in 1984, after 40 days of round-the-clock observation and waiting. Births of *R. djiddensis* and *A. narinari* were filmed on 8 mm movie film by the aquarium staff in 1978 and 1982. Birth and subsequent mating behavior of *A. narinari* were photographed in 1979. Sharks (*T. obesus* and *C. plumbeus*) were always born in a tail-first and abdomen-up position in normal birth. Rays (*A. narinari*) were born head-first or tail-first, always with an abdomen-down position. On four occasions, three births were tail-first and one was head-first. In *R. djiddensis* one pup was born tail-first.

Triaenodon obesus—A tank-born female gave birth to two young during the night of 24 September 1987. We first discovered a newborn shark in the tank and the mother, swimming faster than usual, about 0.6 m above the bottom, with the tip of the tail of a second shark protruding from her cloaca. It was born seconds later and was immediately netted and transferred to a nursery tank. A mature tank-born male chased the mother shark, swimming just behind her during the birth. The first-born shark was found the next morning, alive, lying hidden in a rock crevice. New-born sharks of this species usually do not go to the surface just after birth but swim near the bottom, possibly in search of refuge.

Carcharhinus plumbeus

Case 1—A female shark (No. CP-1), TL 190 cm, BW ca. 60 kg, which had been kept for four years and eleven months in captivity, gave birth to eight young on 18 July 1984. (She was probably fertilized by males kept in the same tank in 1983. Mating had not been observed during this period, but fresh mating scars were found in the summer of 1983.) The cloaca of this female was slightly open

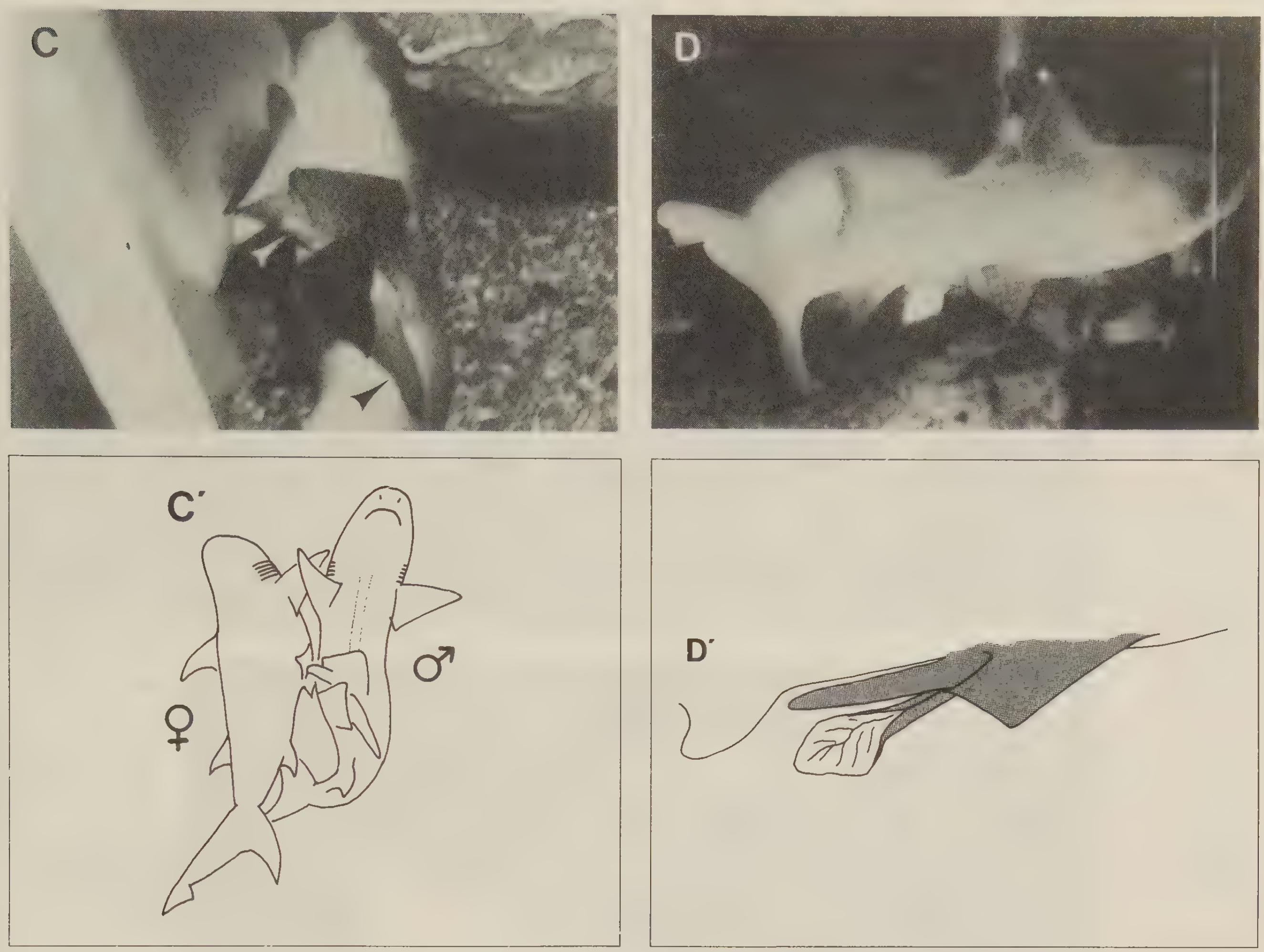


Figure 5. (continued)
C, C′, Lying on his back on gravel tank-bottom, the same male is inserting his left clasper at 90° angle to his body axis (white arrow). Right clasper is in usual position (black arrow). Female's right ventral fin is to the upper left of inserted clasper. D, D′, After 1.5 min of insertion the male withdrew his clasper and swam away (tip of used left clasper is spread and bent slightly downward).

at 20:30 and closed at 21:00. It was open again at 21:30 and birth started at 21:40. Before birth, she swam at mid-depths (2 m) in the tank at normal speed, but during birth she skimmed the bottom swimming faster than usual. The first newborn shark emerged tail-first and abdomen up (normal orientation). Immediately after birth it was attacked and eaten by a male *C. leucas* which had been in the tank for six years (TL 3 m, BW ca. 250 kg). After a few minutes, the tailtip of a second baby, and, briefly, the shorter portion of the tail of a third, protruded. The second shark was born tail-first and abdomen up several minutes after tip protrusion. It swam vertically up to the surface. The third birth took about 40 minutes from initial tip protrusion to discharge and resulted in a stillborn pup. This fetus was born tail-first and abdomen down, with its umbilical cord and fetal placenta trailing rearward. Except for the first (eaten) and the third (stillborn), the remaining six sharks experienced a normal, tail-first birth with the abdomen up or slightly lateral (Fig. 10A, B). All six were picked up in a healthy condition by the aquarium staff. Duration of birth was close to six min for one shark, and the same or slightly shorter for the others. The entire process of delivery took about 1 h and 40 min, including the 40 min of the stillbirth. Three individuals of these original six have survived for three years as of July 1987. Before the first birth, two males of *C. plumbeus* chased the pregnant female for about 10 minutes. During birth they chased her one at a time, but not as eagerly as before. In contrast to the behavior of *T. obesus* and *A. narinari* to females giving birth, *C. plumbeus* showed neither attack behavior toward the young during birth nor mating behavior during or after birth. Three weeks before the 1984 birth, the pregnant female showed a diminished appetite which continued until she gave birth. Two days after

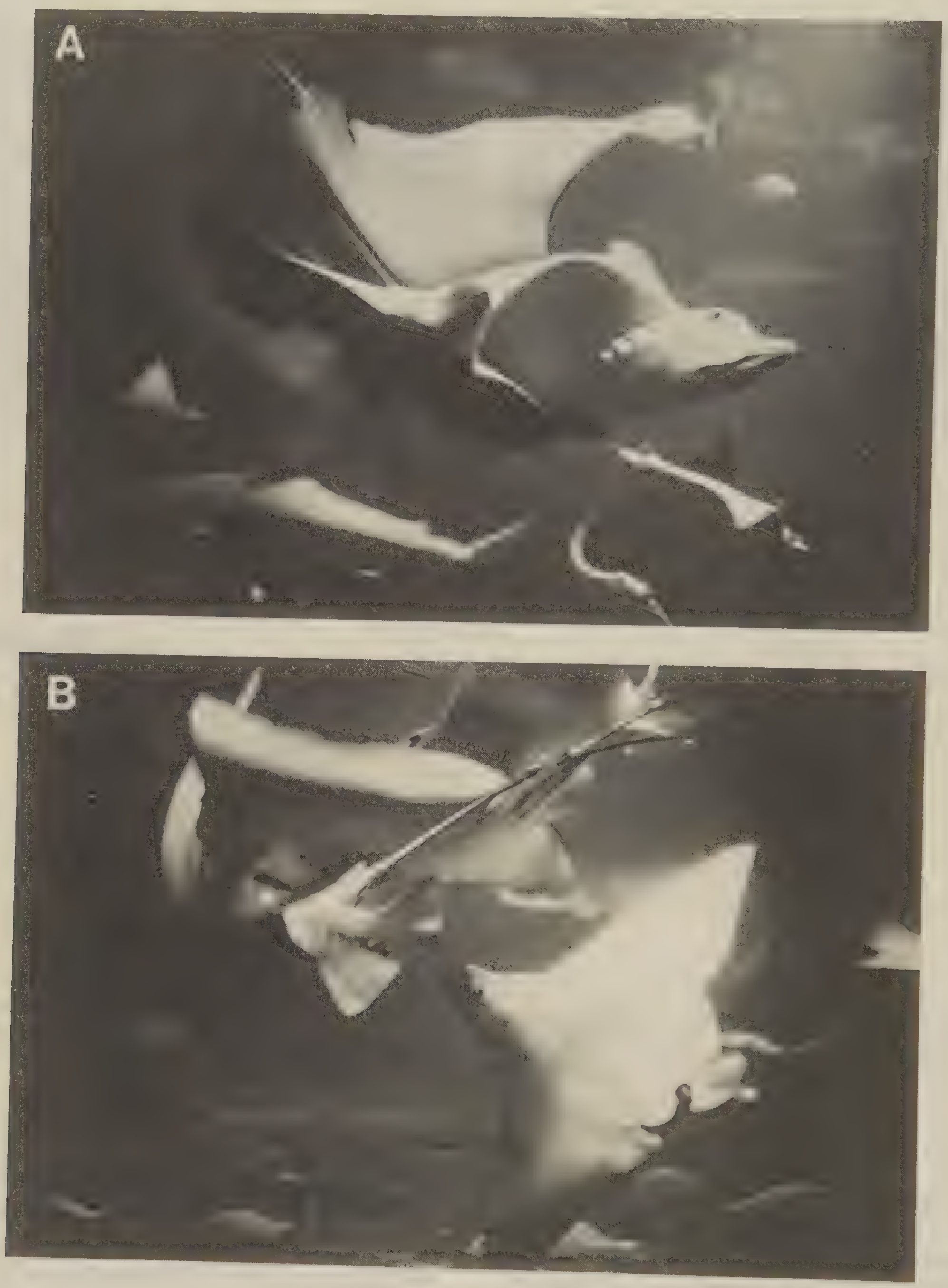


Figure 6.
Copulation of *Aetobatus narinari*, 3 September 1979. A, Male (left and on his back) biting a female (bigger, right) on front margin of right pectoral fin, inserting clasper in abdomen-to-abdomen posture, and ejecting semen. Semen is seen leaking from groove of inserted clasper. Semen is visible as a white cloud below male's left black pectoral fin. Upper white is belly of another male nibbling the dorsal surface of the female. B, Copulation after Fig. 6A, male (far right) bites the rear edge of female. Note his right clasper is bent ventrally, possibly preparatory for insertion. On top is a male storming to nibble female; second from top is another male nibbling the female's dorsum and third is the female, her spotted left ventral fin clearly visible. White cloud below right pectoral fin of second male is semen leaking from clasper, probably from a preceding copulation. C, Dorsal view photographed just after 6B. Male biting right pectoral fin of female, attempting abdomen-to-abdomen posture. He inserted his clasper (perhaps the right) after the photograph was taken. Two males in upper left corner are individuals seen first and second from the top in B.

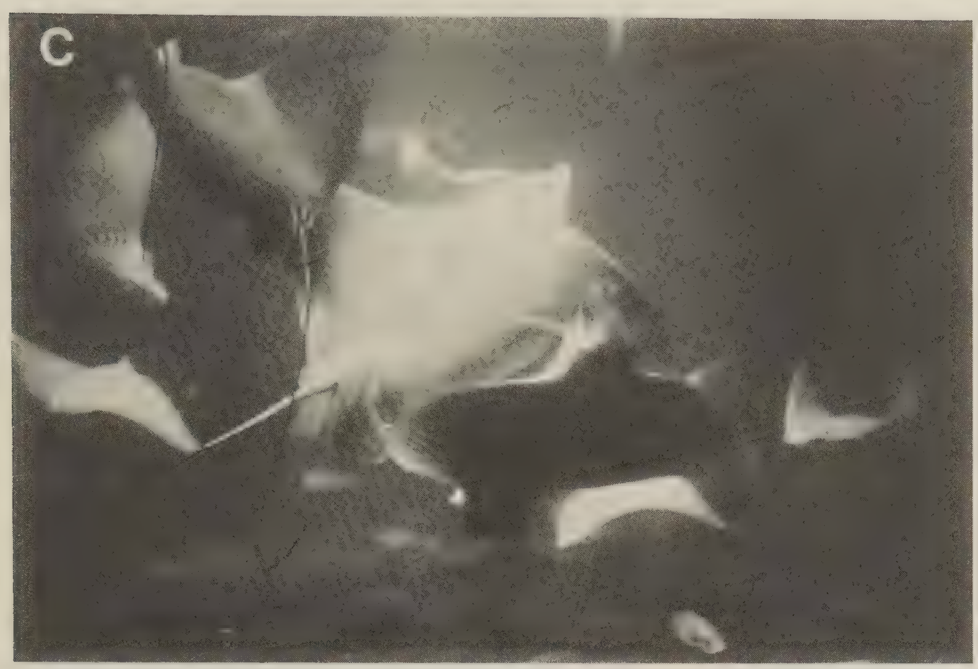
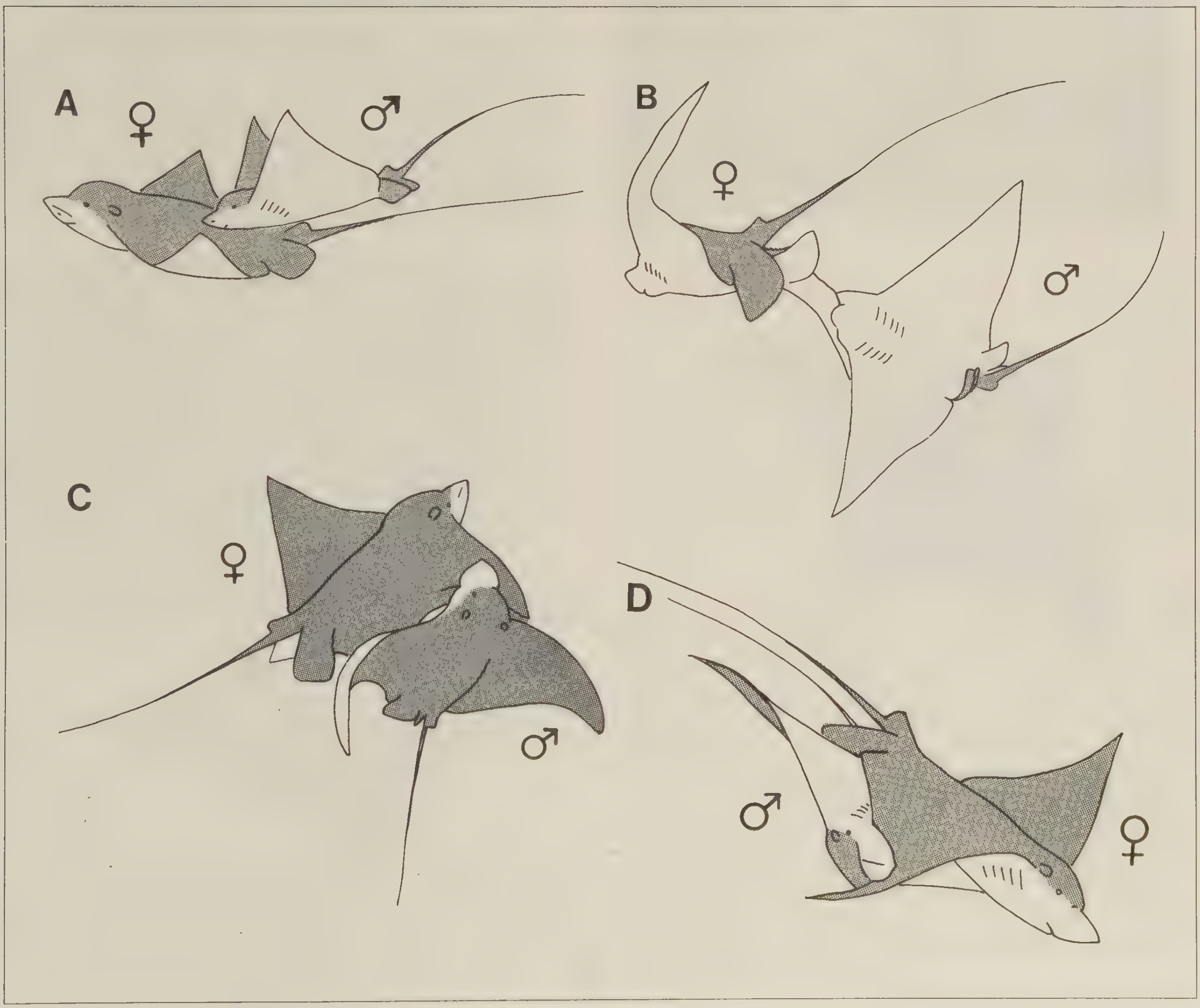


Figure 6. (continued-left)

Figure 7. (below)
Typical pattern of mating behavior of *Aetobatus narinari*. A, After chasing female, male nibbles her dorsal surface. Female stops swimming to begin copulation. B, Male bites female on pectoral fin (left or right, front or rear margin). In some cases either clasper is bent ventrally at this stage, preparatory for insertion. C, Biting female's pectoral fin, the male attempts to attain an abdomen-to-abdomen posture for insertion. D, Male biting the female's pectoral fin, abdomen-to- abdomen posture. Male inserts either clasper into female cloaca; usual position male below, in mid-depths of tank.



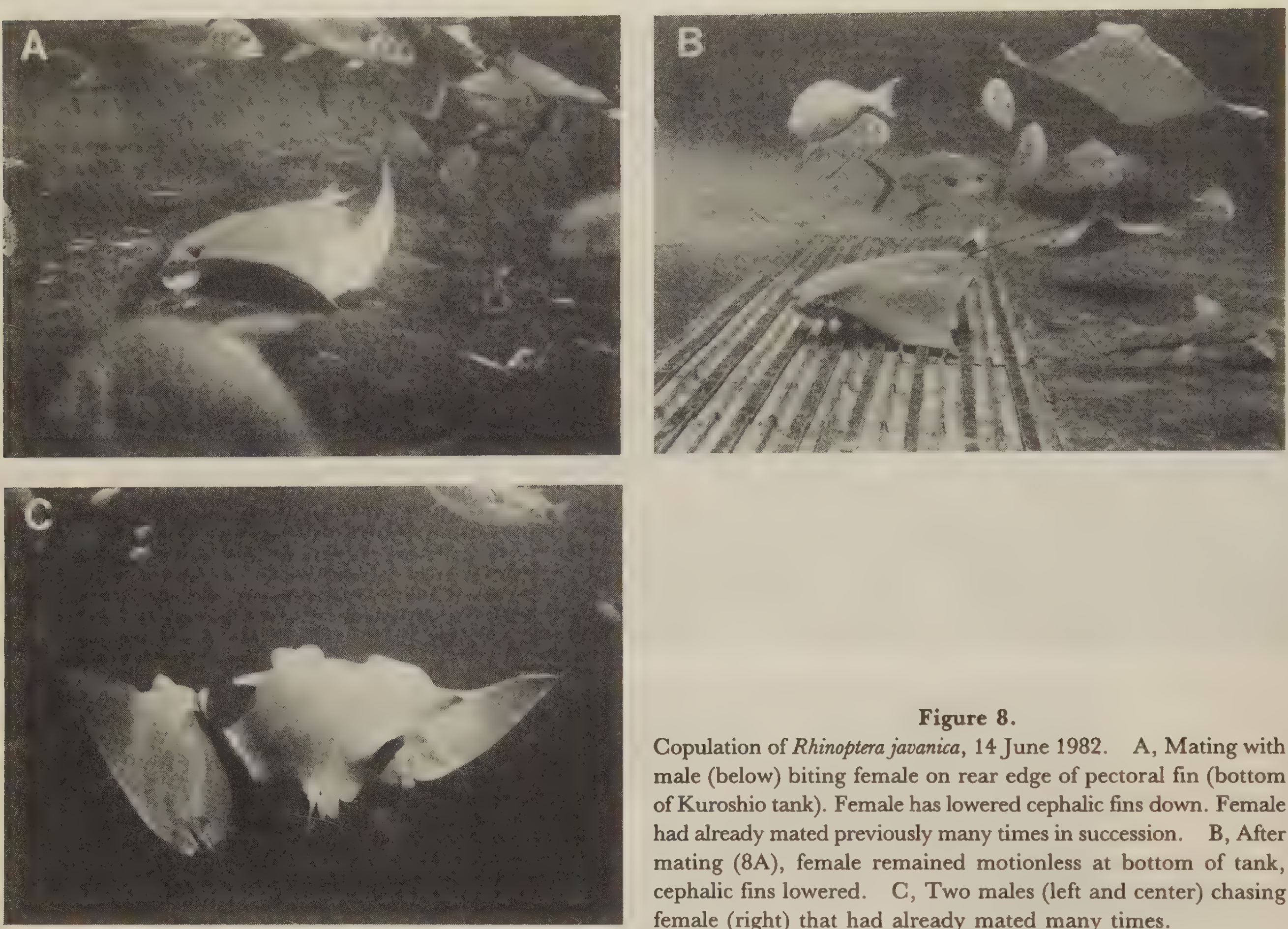


Figure 8.
Copulation of *Rhinoptera javanica*, 14 June 1982. A, Mating with male (below) biting female on rear edge of pectoral fin (bottom of Kuroshio tank). Female has lowered cephalic fins down. Female had already mated previously many times in succession. B, After mating (8A), female remained motionless at bottom of tank, cephalic fins lowered. C, Two males (left and center) chasing female (right) that had already mated many times.

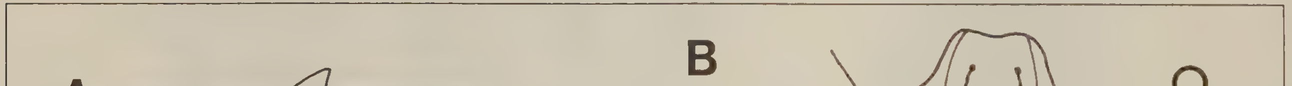


Figure 9.
Copulation of *Rhinoptera javanica*, 1979. A, Male inserting clasper in abdomen-to-abdomen posture from beneath female. B, Pair swivelling horizontally, 180° on axis of inserted clasper.

Table 14.
Data on parturition of elasmobranchs observed at the Okinawa Expo Aquarium, September 1978–September 1987.

Species	Date	Birth presentation	Duration of parturition/1 fetus
Triaenodon obesus	11 August 1987	Tailfirst, abdomen-up	—
	24 September 1987	Tailfirst, abdomen-up	ca. 1 min
Carcharhinus plumbeus	18 July 1984	Tailfirst, abdomen-up	ca. 6 min (1 h 40 min/9 fetuses)
	13 August 1987	Two tails together	Stillbirth picked
Rhynchobatus djiddensis	19 September 1978	Tailfirst, abdomen-up	ca. 3 min
Aetobatus narinari	3 September 1979	First fetus, headfirst, abdomen-down	2–3 min
		Second fetus, tailfirst, abdomen-down	3–4 min
	13 August 1982	First fetus, tailfirst, abdomen-down	1 min 25 s
		Second fetus, tailfirst, abdomen-down	50 s

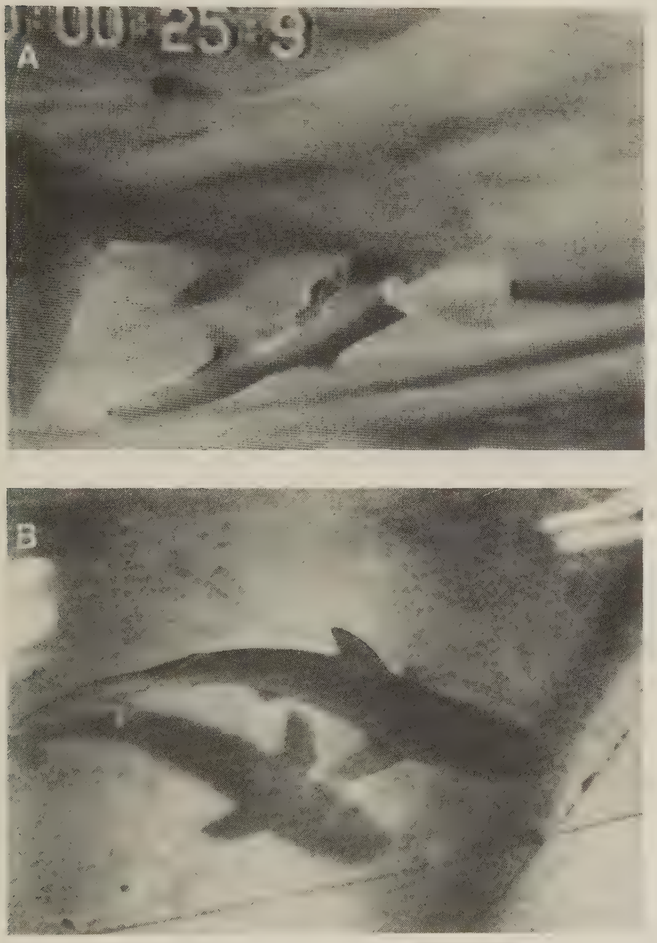


Figure 10.
Birth of *Carcharhinus plumbeus*, 18 July 1984. A, Tail of first fetus protruding, abdomen-up position. B, Newborn pup photographed one day after birth.

giving birth, her appetite returned to more than its previous level. Intake of food in the first week after giving birth was 16% of her body weight, compared to 7% per week before giving birth.

Case 2—A second female shark, CP-6, in the Kuroshio tank (TL 185 cm and BW 46 kg) was attacked in the abdomen, exposing the internal organs, on 22 June 1986. The attacker was not identified but presumed to be a *C. leucas*, *C. obscurus*, or male *C. plumbeus*. (The female was already pregnant at time of capture on 14 September 1985.) We transferred the wounded female to a reserve tank and removed ten fetuses by dissection (Fig. 11A, B). As they were near full-term, and six out of ten shark pups survived, we assumed that had she not been attacked, we would have observed normal birth of her pups in our tank.

Case 3—On 13 August 1987, tails of two fetuses were noticed protruding from the cloaca of a female *C. plumbeus* (No. CP-7, 1.9 m TL and ca. 60 kg BW, captured on 21 July 1986). After beginning birth, she was attacked and bitten by a *C. leucas* around the second dorsal fin (Fig. 12A, B). She was transferred to a reserve tank, and nine still-born fetuses were removed from the cloaca (Fig. 12C). Cause of death is unknown. Whether the two tails protruding together caused the stillbirths or whether the fetuses had already died in the uterus causing the two tails to protrude together is also unknown. The wounded adult shark was returned to the exhibit tank two weeks later and within one month had recovered completely from the attack.

Rhynchobatus djiddensis—A female of *R. djiddensis* (TL 270 cm, BW 97 kg) gave birth prematurely to eight pups on 19 September 1978. Birth began at 08:30 and ended at 10:00. She skimmed the bottom of the tank so closely that the tail of a fetus projecting from the cloaca occasionally touched it, making observation of birth difficult. Birth of one of the eight pups was observed. It was born tail-first and abdomen up, its delivery taking about three minutes. All eight pups were released with yolk sacs of about six cm diameter and died the next day. Their total length varied from 43 to 46 cm, much shorter than the 51 to 54 cm length of the six individuals born earlier, which survived for 11 months.

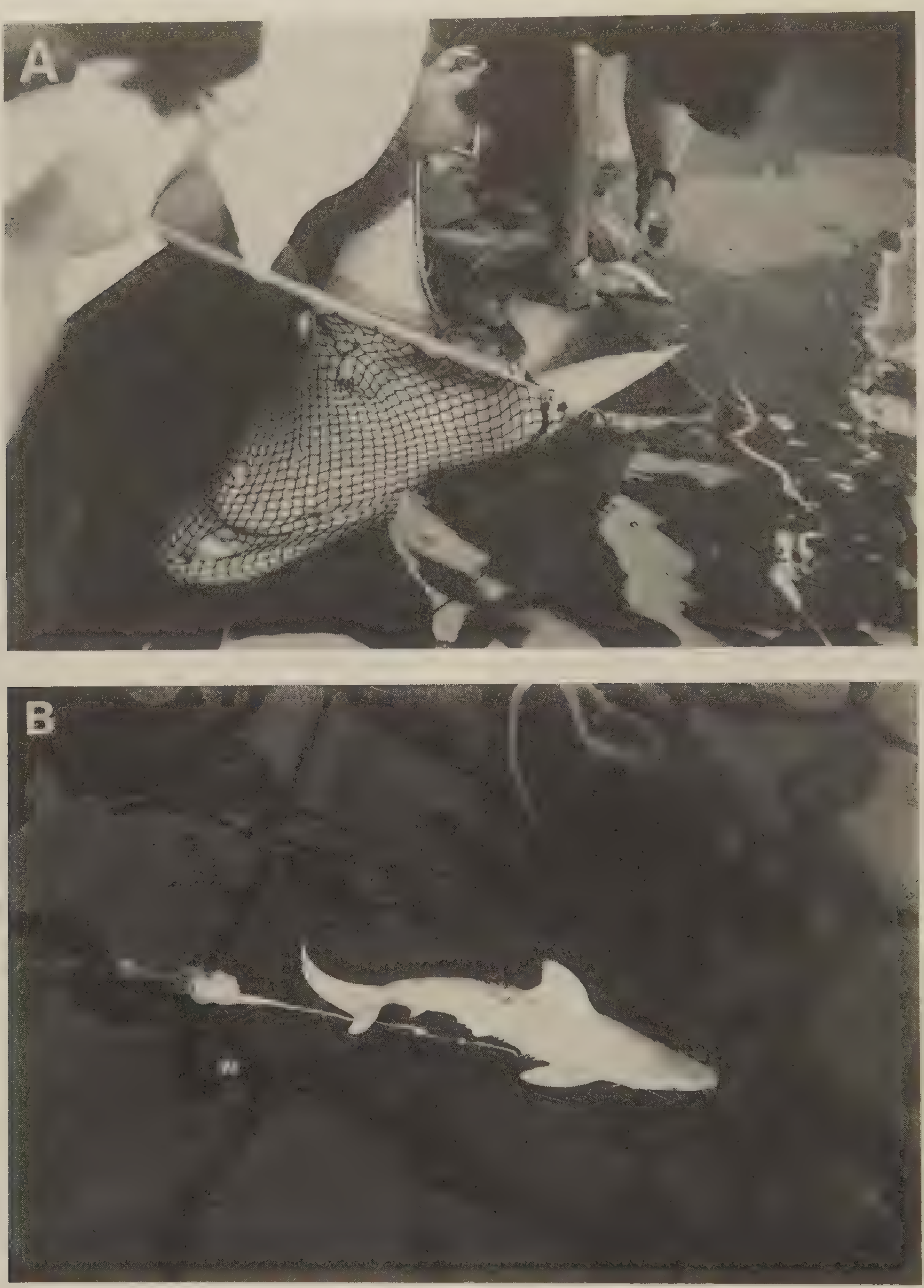


Figure 11.
Delivering pups from pregnant and dying mother of *Carcharhinus plumbeus* by caesarian section, 22 June 1986. A, Gravid female transferred to reserve tank, ten pups removed (mother's head restrained by dip-net). B, One of six surviving pups. All were full-term and swam immediately, some of them with umbilical cord and fetal placentum still attached and trailing. Placenta fell off within a day.

Aetobatus narinari—Observations of birth in *A narinari* were made on two occasions. On 3 September 1979, at 16:20, dark red material was seen in the cloaca of a pregnant *A. narinari* (Fig. 13A). At 21:30 males began chasing her; it appeared to be premating behavior. She jumped out of the water at 22:30, in the course of being chased by three males actively courting her. The dark red material disappeared from view into the cloaca, and the swelling of the abdomen shifted toward the cloaca at 22:40. Then the dark red material appeared again, and at 22:45 the snout and eyes of the first pup were seen in the midst of it (Fig 13B). A few minutes later the pup was born head-

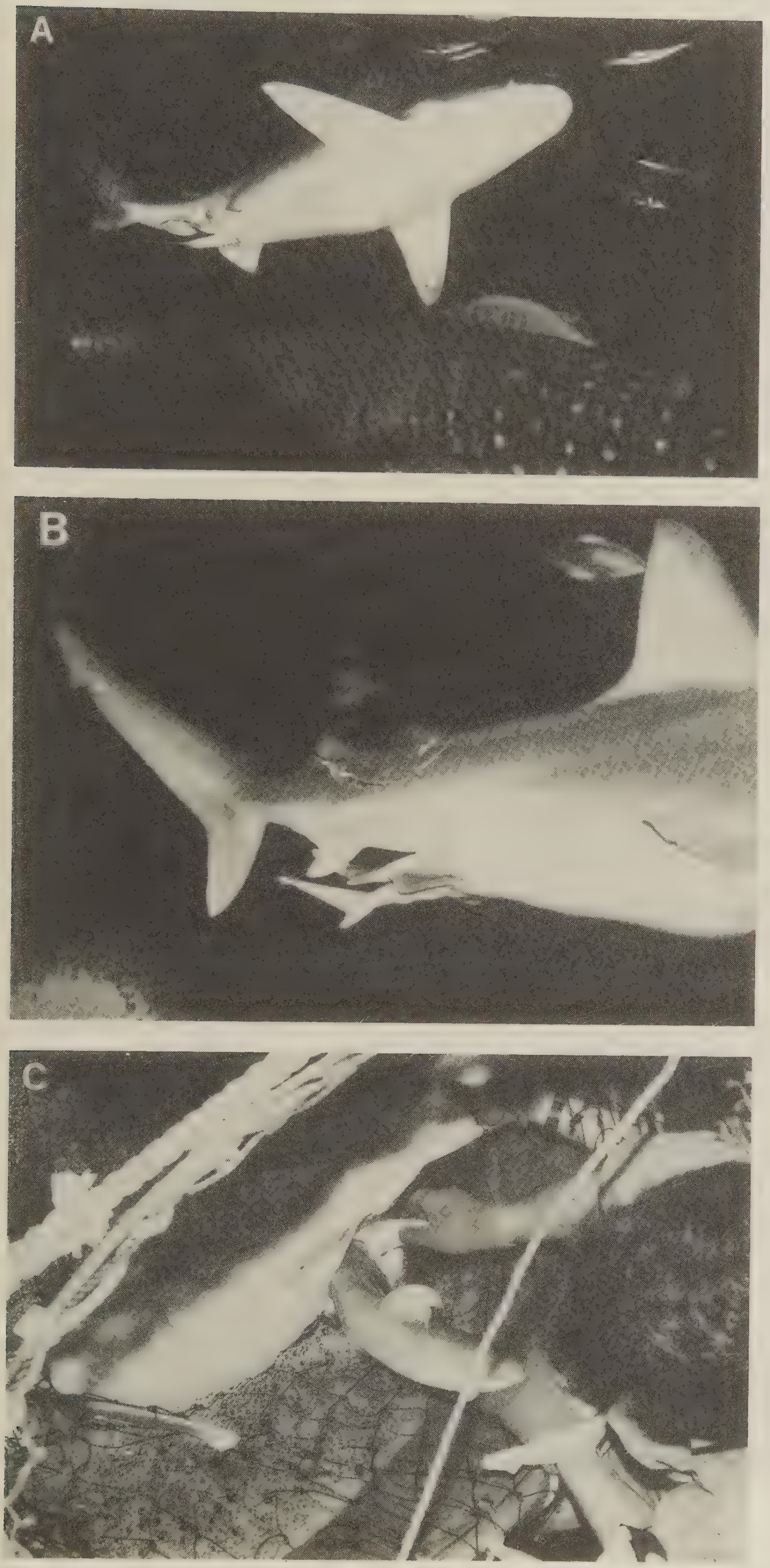


Figure 12.

Stillbirth of *Carcharhinus plumbeus*, 13 August 1987. A, Tails of two fetuses, abdomens down, protruding from the cloaca of female (No. CP-7). 5.17 m long whale shark, *Rhincodon typus*, visible below. B, After starting birth, this female was attacked and bitten by *C. leucas* around second dorsal fin. C, Removing one of nine fetuses from her cloaca, in the reserve tank. The embryos died but the mother survived.

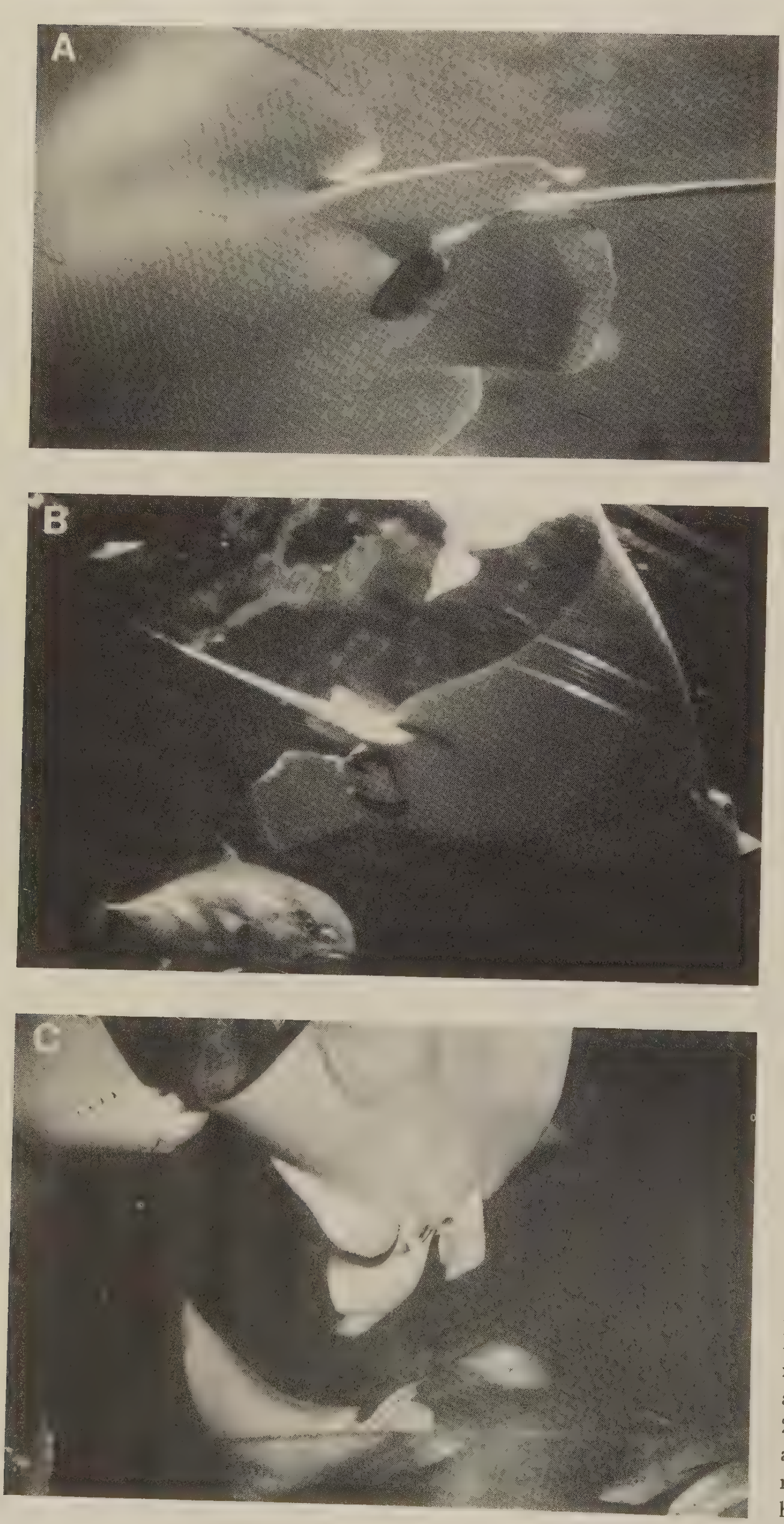


Figure 13.

Birth of *Aetobatus narinari*, 3 September 1979. A, Dark red material was seen in the cloaca of the pregnant female at 16:20. It disappeared to reappear around 22:40. B, Snout and eyes of the first pup, 22:45. C, Minutes later, a pup is born head-first and abdomen down (center). Top center is the mother, top left and bottom are males who chased her before birth.

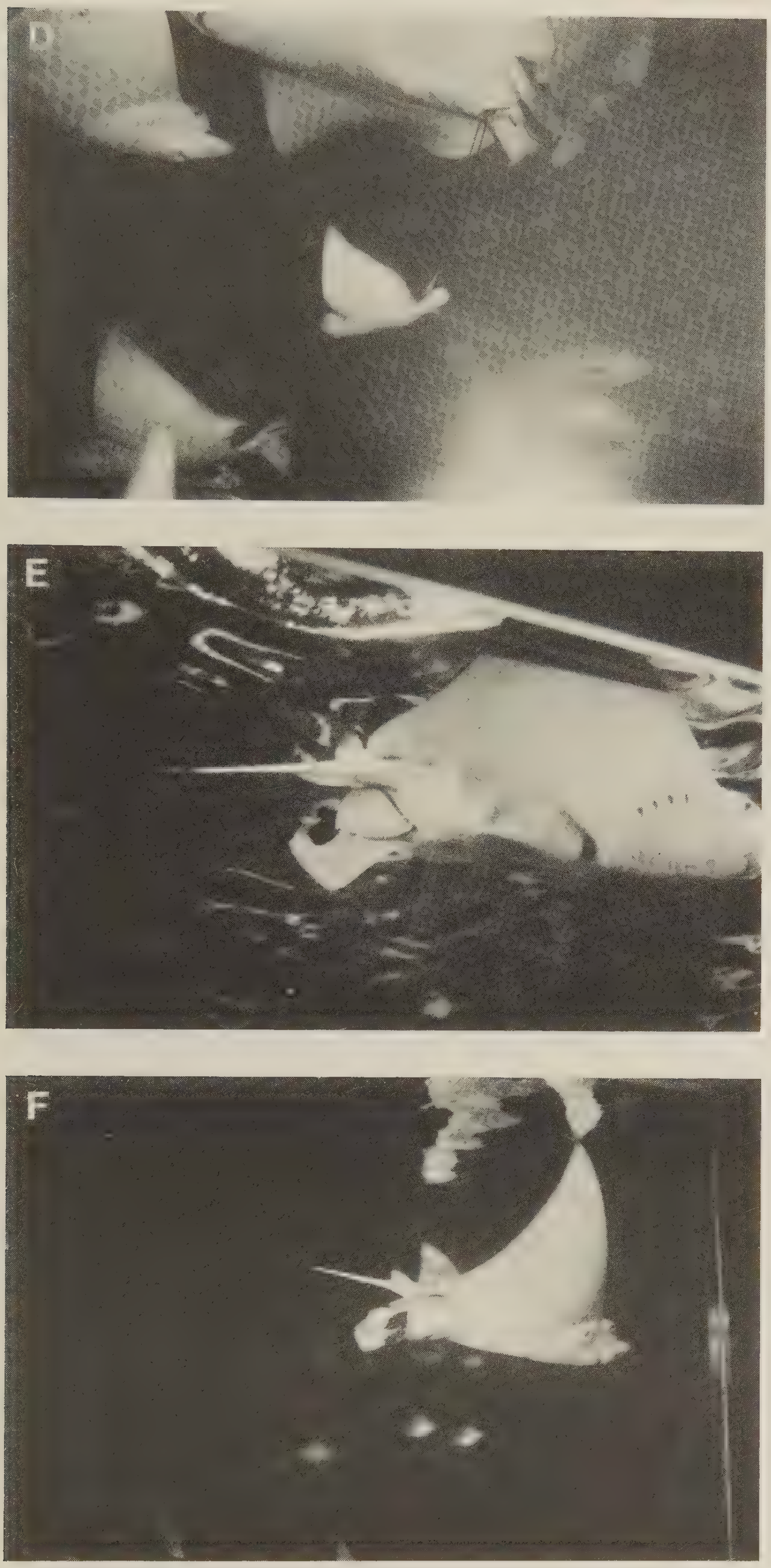


Figure 13. (continued)
D, Pup (center) parting from mother (top center), its tail tip is still in her cloaca. At top and bottom left are males. E, Second pup, one minute after first birth, coming out tail-first and abdomen down. Notice concave belly of mother because of emptied uterus and possibly, laboring of muscles to squeeze pup out. F, Last stage of second birth. Pectoral fins of pup are wrapped upward.

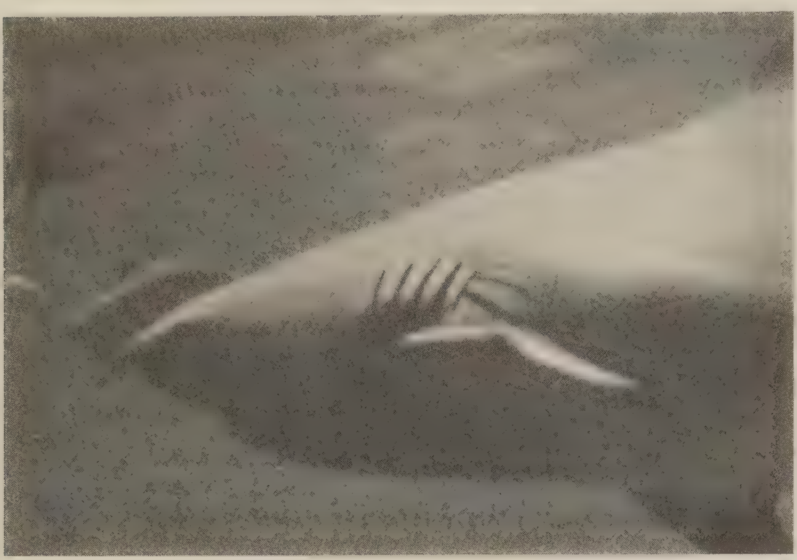


Figure 14.
Male *Carcharhinus leucas*, TL 3 m, BW ca. 250 kg, the most effective attacker in Kuroshio tank, with looped tail of newborn pup of *Aetobatus narinari* projecting from 5th gill slit on left side, indicating previous night's attack.

first, and abdomen down (Fig. 13C, D). About one minute later, the tail of a second pup was seen, and it was born tail-first and abdomen down a few minutes later (Fig 13E, F). The mother was swimming slightly faster than usual at middepth (2 m) in the tank during the births. At 23:00 copulations with three or four males began (see Observations on Mating). The second observation of birth in this same *A. narinari* was made on 13 August 1982. In this instance, 2 pups were born tail-first and abdomen down, contrary to our expectations. (The head of this species being much thicker than the body, we had expected birth to reflect an "in utero" arrangement of the head of one fetus to the tail of the other.) On 11 July 1983, this fecund mother gave birth to two pups again. Although birth was not observed, we noticed her concave abdomen the following morning, and the tail of a baby *A. narinari* projecting about 20 cm from the fifth gill slit on the left side of *C. leucas* (Fig. 14), and another tail trailing about 30 cm from the mouth of a *Galeocerdo cuvier*.

Second-Generation Captive Birth

Scyliorhinus torazame—A tank-born eight-year-old shark (TL: 47 cm, BW 430 g) began to lay eggs on 20 October

Table 15.
Data on the second generation captive birth of *Triaenodon obesus*. TL = Total length; BW = Body weight.

		Size and weight			
		Mother		Father	
	Date and period	TL (cm)	BW (kg)	TL (cm)	BW (kg)
Birth of parents (born in the same litter)	19 June 1977	69	2.0	66	1.4
Period of maturity	6 years				
First mating observed	27 June 1983	135	ca. 18	142	ca. 20
Gestation period	405 days				
		Young (male)			
		TL (cm)	BW (kg)		
Parturition of the pup	6 August 1984	60	ca. 0.8		
	171 days				
Measurement of the pup	23 January 1985	69	2.2		
	523 days				
Death of the pup	11 January 1986	100	3.9		

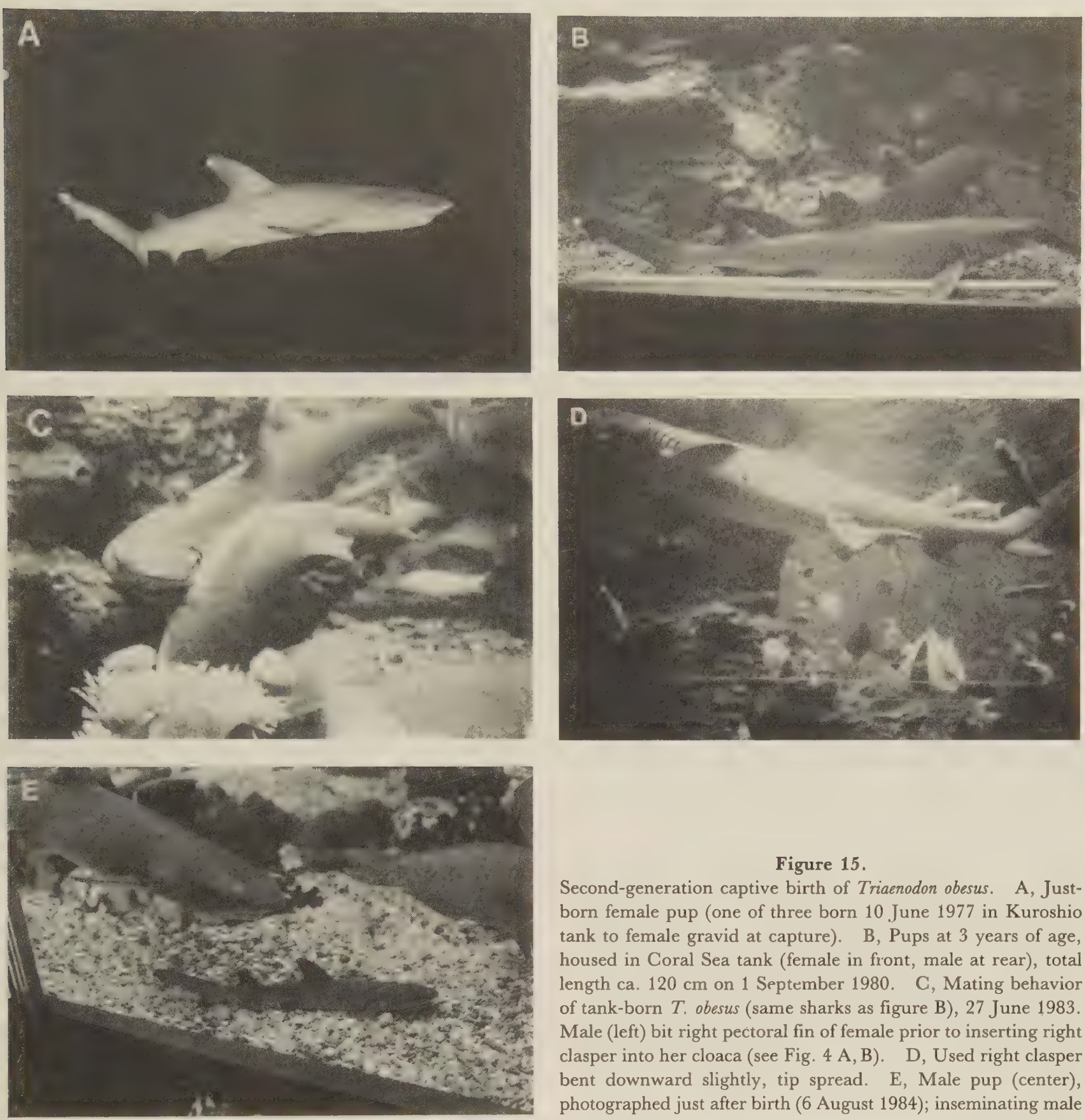


Figure 15.
Second-generation captive birth of *Triaenodon obesus*. A, Just-born female pup (one of three born 10 June 1977 in Kuroshio tank to female gravid at capture). B, Pups at 3 years of age, housed in Coral Sea tank (female in front, male at rear), total length ca. 120 cm on 1 September 1980. C, Mating behavior of tank-born *T. obesus* (same sharks as figure B), 27 June 1983. Male (left) bit right pectoral fin of female prior to inserting right clasper into her cloaca (see Fig. 4 A, B). D, Used right clasper bent downward slightly, tip spread. E, Male pup (center), photographed just after birth (6 August 1984); inseminating male is at top left.

1984. She laid eight eggs from October 1984 to February 1985. These eggs, as well as other eggs laid after that time, failed to hatch.

Triaenodon obesus—A tank-bred seven-year-old *T. obesus* female gave birth to a pup on 6 August 1984 (Table 15, Fig. 15). This birth was the result of mating between parents from the same litter. The pup died at the age of one year and five months. See Discussion section for speculation about the cause of death.

Gestation and Incubation Periods

Scyliorhinus torazame—The incubation period for the egg of this species ranges from one year twenty-six days to one year six months, with an average of one year three months (Table 16). Incubation period apparently varies with water temperature. The relatively long incubation period at our aquarium is likely a consequence of the cool temperature in our tank (about 11°C, see Table 5).

Table 16.
Gestation and incubation periods of elasmobranchs at the Okinawa Expo Aquarium. TL = Total length; BW = Body weight.

	Mother			Gestation and incubation period (d)				Water temperature in tanks (°C)	
Species	No.	TL (cm)	BW (kg)	*N*	Range (d)	Average (d)	Remarks	Range	Average
Scyliorhinus torazame	1	50	0.63	14	418–513	466	Spawning from Jan. to Dec. 1982	9.1–13.7	11.3
	2	47	0.53	10	391–538				
	3	44	0.53	13	410–510	472			
Triaenodon obesus	1	135	ca. 18	1	405		Birth Aug. 1984, tank-born mother	19.9–30.2	24.7
	2	122	ca. 10	1	392		Birth Sept. 1987, tank-born mother		
Carcharhinus plumbeus	1	190	ca. 60	2	ca. 400		Birth July 1984 and June 1986 Period from time of mating scars observed to birth	19.8–29.6	24.6
Aetobatus narinari	1	DW ca. 140	ca. 60	9	331–377	356	Period from birth to next birth	19.8–29.6	24.6

Triaenodon obesus—Gestation periods of this species were calculated from the dates of observed copulation (shark No. 1) and the fresh mating scars on the gill slits (shark No. 2), to their respective dates of birth (Table 16).

Carcharhinus plumbeus—We did not observe mating in this species, although fresh mating scars on the left pectoral fin and gill slits were noticed many times. The gestation period of about 400 days was determined in two cases from the date of finding fresh mating scars.

Aetobatus narinari—We observed birth and immediate subsequent copulations of *A. narinari* in 1979, and fresh mating scars on the dorsum of a female the day after delivery in July 1985. Mating the day after birth was not observed. We have inferred from these observations that mating and fertilization occurs just after birth. Therefore, in the ten observations made from 1976 to 1985, gestation periods were counted from birth to subsequent birth.

Breeding Seasons in Captivity

Breeding seasons in 14 species observed at the OEA are shown in Figure 16. Hatching was observed in four egg-laying species (*H. japonicus*, *C. umbratile*, *S. torazame*, and *O. japonicus*) and birth was observed in nine species (Fig. 16). The *R. djiddensis* pups born in September were much smaller than those from a litter born in October and had a large, unabsorbed yolk sac. Therefore, it is likely that those born in September were premature and that the natural birth season is October. The birth of *D. sephen* pups in October was also premature, indicating that the normal birth season may be later in the year.

Discussion

Information on reproduction of elasmobranchs in captivity is now available from Japan and the rest of the world (Tables 1–4), yet little is known about the survival and growth of pups born or hatched in captivity. Successful breeding, as the term is used here, means that newborn or hatched pups are kept until they attain maturity and breed to produce their own pups. From this viewpoint, successful breeding at the OEA has occurred only in *T. obesus*.

At the Okinawa Expo Aquarium, sharks showed better breeding results than rays. The reasons for this may be habitat conditions and food problems. For long-term survival and consequent reproductive success, rays of the Dasyatididae may need a sand layer on the bottom of their tank, which our tank did not provide. Rays in general are thought to eat many kinds of molluscs and crustaceans. The food given to the sharks and rays in the exhibit tanks may not be sufficient in either quantity or quality for these two groups of food-animals. Attempts to feed as many kinds of animal food as possible to newborn pups of *A. narinari* kept in reserve tanks have all ended in failure. Most likely, the food thus far provided for both the young and the parents of this species is still not adequate for their needs. Among the sharks bred in our aquarium, females of *C. umbratile*, like *S. torazame*, produce eggs all year round, but the hatch-rate of the eggs is very poor. Likewise, the sharks captured at depths of 400 to 500 m and housed in our deep sea tank do not live for a very long time. We think the cause of our low success in maintaining and breeding this species results from a water temperature that is too cold. Water temperatures at capture sites (400 to 500 m) range from 14°C to 17°C, whereas the temperature range in our tank is 9.1°C to 13.7°C. Successful hatching of this species has

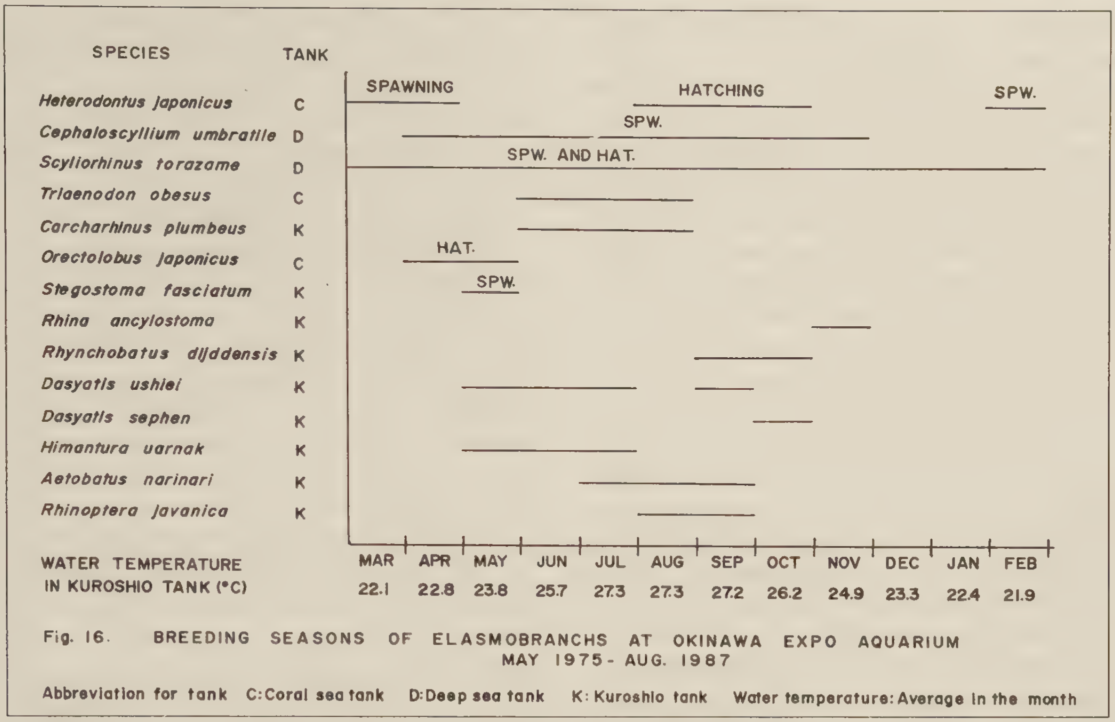


Figure 16.
Breeding seasons of elasmobranchs at Okinawa Expo Aquarium, May 1975–August 1987.

occurred at other aquaria in Japan where the water in which they were kept is warmer than ours. Therefore, we are now experimenting in our reserve tanks with warmer water temperatures.

Mating

Observations of mating in elasmobranchs have been reported for few species. According to Klimley (1980), "brief, incomplete observations" of mating behavior in sharks have been reported for nine species and figured with photographs, diagrams, or illustrations for four species. The nine species reported are *Heterodontus francisci*; *Ginglymostoma cirratum*; *Cetorhinus maximus*; *Scyliorhinus canicula*; *Carcharhinus melanopterus*; *Carcharhinus* sp.; *Negaprion brevirostris*; *Triaenodon obesus*; and *Mustelus canis*. The 4 species figured are: *H. francisci*; *S. canicula*; *C. melanopterus*; and *C. plumbeus*. In addition to these cited by Klimley, mating in *Triakis scyllia* (Tsutsumi 1979), *Scyliorhinus torazame* (Uchida 1982), and *T. obesus* (Uchida 1982; Tricas and LeFeuvre 1985) were also reported with diagrams or photographs. Klimley (1980) reported courtship and copulation in *G. cirratum* in captivity with detailed diagrams, and Rouse (1985) presented photographs of mating of the same species in the sea. In the OEA, a male *S. torazame* showed wrapping posture around a female during mating. This behavior resembles that reported for *S. canicula* (Bolau 1881; Hardy 1959), but the curvature of the male was less than that of *S. canicula*.

The males of *T. obesus* in this report and previous ones (Uchida 1982; Tricas and LeFeuvre 1985); *H. francisci* (Dempster and Herald 1961); *T. scyllia* (Tsutsumi 1979); and *G. cirratum* (Klimley 1980; Rouse 1985) did not assume a wrapping posture in their mating but instead took a parallel position, biting females on their pectoral fins to hold them and insert their claspers.

Reports on the mating behavior of skates and rays are also rare. Observations were reported for *Raja eglanteria* (Libby and Gilbert 1960; Price 1967); *Urolophus concentricus* (McCourt and Kerstitch 1980); *U. jamaicensis* (Dugger 1987); *U. aurantiacus* (Tasaka 1986); *Dasyatis americana* (Brockman 1975); *D. akajei* (Tasaka 1986); *Aetobatus narinari* (Tricas 1980; Uchida 1982); *Myliobatis californica* (Tricas 1980); and *Rhinoptera javanica* (Uchida 1982). In these reports photographs of mating were provided for *U. concentricus* (McCourt and Kerstitch 1980); *U. aurantiacus* (Tasaka 1986); and *U. jamaicensis* (Dugger 1987); and diagrams for *D. akajei* (Tasaka 1986); *M. californica* (Tricas 1980); *A. narinari* (Uchida 1982); and *R. javanica* (Uchida 1982). The photographs and diagrams show abdomen-to-abdomen posture for mating in *U. concentricus*, *U. jamaicensis*, *D. akajei*, *A. narinari*, and *R. javanica*; the male mounting the female, i.e., male's abdomen to female's dorsum in *U. aurantiacus*; and male's dorsum to female's abdomen with a clasper erected upward in *M. californica*. In our observations of *A. narinari* and *R. javanica*, mating posture was always abdomen-to-abdomen, and many males made a rush to copulate with a single female. Consequently, in these two species one female mated with many males, sometimes during a very short time. In *R. javanica*, mating resulted in a strange "ejection" of semen from the female's cloaca and occasional death from severe bite wounds. The ejection was likely the result of an excess quantity of semen introduced into the female by several males during prior copulations (see Observations on Mating—*R. javanica*).

Birth

Reported observations of "natural births", i.e., normal births in the wild or in captivity, not abortion or near-term births stimulated by capture, are extremely rare. Gilbert (1981) reported head-first birth in *Odontaspis taurus* but gave few details. From our observations of birth in *T. obesus* and *C. plumbeus*, normal presentation of pups at birth may be tail-first and abdomen-up, but in *A. narinari* tail-first or head-first and abdomen-down. Further observations, species by species, are needed to draw conclusions about the normal presentation of elasmobranch young. The length at birth of *T. obesus* has been reported to be 55 to 60 cm (Johnson 1978), 52 to 60 cm (Fourmanoir 1961, cited in Randall 1977); and 59 cm (Randall 1977). Length of *T. obesus* in the OEA was 59 to 69 cm, averaging 63.1 cm, slightly longer than in the previous reports. Whether this increase is because of sufficient nutrition for the mother sharks in captivity or whether the difference depends on the geographic distribution is unknown. There is a strong possibility for the former, as discussed later (see Second-Generation Captive Birth). The length of *Carcharhinus plumbeus* at birth is 56 to 64 cm in the western Atlantic (Springer 1960), 65 to 75 cm in the East China Sea (Taniuchi 1971) and 60 to 65 cm in the southwest Indian Ocean (Bass et al. 1973). Our *C. plumbeus* were born 60 to 70 cm long, a little shorter than the length reported from our area by Taniuchi (1971). We removed nine stillborn fetuses from a female *C. plumbeus* (No. Cp-7) who had been attacked by a *C. leucas* around the second dorsal fin (See Observations on Birth—*C. plumbeus*). The average total length of the fetuses was 67.3 cm, ranging from 64 to 70 cm, and the average body weight was 1.8 kg. These values were about the same as those of newborn pups in the two cases previously mentioned in the text. (The eight pups of No. Cp-1 averaged 66.7 cm in total length and 1.63 kg in body weight, ranging 63 to 70 cm and 1.5 to 1.9 kg, respectively; the ten pups of No. Cp-6 averaged 62.5 cm and 1.60 kg, ranging 60 to 66 cm and 1.5 to 1.8 kg.) Thus, the nine stillborn fetuses were considered to be full-term, and data on their length and weight were included with the others. Just as size-at-birth in *C. plumbeus* varied with geographical area, number of pups per litter also varied. One to 14 pups per litter has been reported in the western Atlantic (Springer 1960), 6 to 11 in the southwest Indian Ocean (Bass et al. 1973), and 2 to 10 in the East China Sea (Taniuchi 1971). *C. plumbeus* at the OEA gave birth to 6 to 10 pups per litter in four litters. The disk-width at birth in *A. narinari* has been reported to be 29 cm (Gudger 1914, after Coles 1913), and "anywhere between 17-36 cm" (Bigelow and Schroeder 1953). The young born and measured at the OEA were 50 to 59 cm across the disk and 2 to 4 kg in weight ($N = 4$, Table 12), much wider than the values cited above. This difference may indicate regional size differences for this species (Bigelow and Schroeder 1953), or it may result from a larger size of ray when born in small numbers per litter. A fecund *A. narinari* gave birth to 16 pups over nine births from 1977 to 1986, with one pup (twice) and two pups (7 times) per litter, whereas the previously reported number of pups per litter was four (Gudger 1914; Bigelow and Schroeder 1953) and six to ten (Tinker and DeLuka 1973).

Second-Generation Captive Birth

Second-generation captive births of *Triaenodon obesus* occurred three times at the OEA. In the first case, a six-year-old tank-born female mated with a brother born in the same litter and gave birth to one male pup in August 1984, about 13 months after mating and, in the second case, the same female gave birth to three pups in August 1987 (See Observations on Mating, Tables 14, 15). In the third case, an eight-year-old tank-born female gave birth to two pups in September 1987 (See Observations on Birth, Table 14). In the first case, the birth was certainly the result of mating between a female and male from the same litter. The father in the second case was unknown but was one of the female's two brothers, because there were no other mature males. The mother in the third case was the younger sister of the female of the first and second cases. Her partner also had to be either of the two brothers of that female, i.e., brothers two years older than herself. First-generation captive birth of *T. obesus* occurred four times at the OEA from 1977 to 1984 and produced nine pups. Their total length at birth averaged 63.4 cm, ranging from 59 to 69 cm, and body weight averaged 1.2 kg, ranging from 0.84 to 2.0 kg. The second-generation captive birth total length of five of six pups averaged 44.2 cm, ranging from 35 to 60 cm, and body weight averaged 0.39 kg, ranging from 0.25 to 0.8 kg. Survival rate one year after birth was 89% in first-generation captive birth and 50% (excluding two stillbirths) in second-generation captive birth. Whether the lower values for second-generation pups, in length and weight at birth, survival rate, and occurrence of stillbirths were the result of inbreeding or other negative factors derived from captive conditions, or a combination of the two, is unknown. The pup in the first case of second-generation captive birth was the largest of the second-generation captive bred pups in length and body weight. It was 60 cm in total length and 0.8 kg. Born alone, it survived for one year and five months (Table 15). Cause of death is unknown, but we speculate that food problems contributed to it. Both quantity and quality of food may not have been sufficient, especially the quantity in late autumn (November) when the water temperature begins to fall. Inbreeding-depression in land mammals that are kept in captivity for a long time with multiple generations has become a problem in zoos. Survival rate in young pups of mammals born as the result of inbreeding in zoos was reported to be lower than that of those born as the result of noninbreeding (Conway 1979). However, for fishes kept in captivity in aquaria, breeding itself is not easy, much less multiple-generation breeding. Thus, inbreeding-depression is not as yet a big problem for aquarium management, except for a few species of fishes, such as *Hippocampus coronatus*. For *H. coronatus*, multiple-generation breeding has resulted in lowered rates of hatching and survival of hatched fries, and in smaller size of mature fish (R. Kawabe, Shima Marineland, pers. commun., November 1987). Though not yet observed in elasmobranch fishes, inbreeding-depression does probably occur. Because it can be most easily recognized in elasmobranch species that produce a relatively small number of pups and in which adults and pups can be individually identified, such as *T. obesus*, we are planning to introduce wild females of *T. obesus* into our tanks to study the phenomenon. In captivity at the OEA, *Triaenodon obesus* matures at ages six to seven years, at a total length of from 130 to 135 cm for females and 141 to 142 cm for males. Females give birth to from one to three pups from June to September with a gestation period of 12 to 13 months, at intervals of two to three years. The reported sizes at maturity of *T. obesus* are 105 to 109 cm for females, 104 to 105 cm for males (Compagno 1984), and about 130 cm for females (Randall 1977). Randall reported a precaudal length (PCL) of 101.2 cm for the smallest mature female which coincides with about 130 cm total length in his figure showing the relationship of precaudal length to total length, but he noted that "small size might be expected." The larger size at maturity of sharks in the OEA may result from our aquarium conditions, including feeding, size of tank, and temperature. We fed *T. obesus* of all sizes daily. In nature they probably do not feed daily and must expend more energy to obtain food than does a captive individual (Randall 1977). The growth rates at several stages of our *T. obesus* are higher than those reported by Randall (1977) for both wild and captive individuals at a laboratory in Israel. Randall's sharks were fed every two or three days in a nine-ton tank, at water temperatures of 21.5°C to 27°C. A male shark of 73 cm PCL (about 96 cm TL) and a female of 88 cm PCL (about 115 cm TL) grew 4 cm per year (male) and 2.3 cm per year (female). At the OEA, a male of 98 cm TL had a growth rate of 16.2 cm per year and a female of 131 cm TL a growth rate of 6.4 cm per year. These individuals were kept in a 200-ton tank with water temperatures of 19.8 to 30.2°C. Although there are differences between the growth rates of precaudal and total lengths, and more errors in measurements of total length than of precaudal length, the growth rates of sharks kept at the OEA appear to be higher than those at the laboratory in Israel. The higher growth rates at the OEA are probably a result of more frequent feeding, more activity in a much bigger tank, and slightly higher temperatures. The growth rates of wild *T. obesus* were reported (Randall 1977) to be from 2.1 to 4.2 cm per year in precaudal length. These rates are from Randall's tagging study on sharks ranging from 81 to 105 cm PCL (107 cm to 131 cm TL). In addition to the reasons mentioned above, it is possible that we misjudged size at maturity, and mating may have occurred at a shorter length. We did not physiologically investigate the maturity of this species; we reported only behavioral observations. Because we did not make round-the-clock observations, it is possible we could have missed ineffective matings or those unaccompanied by mating scars, before the ages of six to seven years old. Judging from mating behavior which we did observe, however, it is unlikely that there is mating without mating scars. There appears to be too little published data on incubation period for *Scyliorhinus torazame*, except for a rough approximation of several months to over one year (Nakaya 1979). Incubation period in teleost eggs varies with water temperature—prolonged at low temperatures and shortened at elevated temperatures (Kawamoto 1977; Hempel 1979). The long incubation periods for this species at the OEA (averaging 1 yr 3 mo and ranging from about 1 yr 1 mo to 1 yr 6 mo) was the result of the low water temperatures in which the egg cases were kept (averaging 11.3°C and ranging from 9.1°C to 13.7°C [Tables 5, 16]). This same species in another aquarium in Japan had an incubation period of seven to nine months at water temperatures averaging 14.2°C (ranging from 10.3°C to 17.2°C) in one tank and averaging 14.5°C (ranging 13.7°C to 16.6°C) in a second tank (S. Tasaka, Shimoda Floating Aquarium, pers. commun., November 1987). These incubation times for *S. torazame* seem to indicate a relationship between incubation period and water temperature. The incubation period in *Scyliorhinus canicula* was reported to be 6.5 to 7.5 months at 14°C (Foulley and Mellinger 1980, cited by Dodd 1983). This value is about the same in both time and temperature as that for *S. torazame* at the Shimoda Floating Aquarium. The gestation period in *Carcharhinus plumbeus* is estimated to be 8 to 12 months in the western Atlantic (Springer 1960), and 11 to 12 months in the southwest Indian Ocean (Bass et al 1973) and the East China Sea (Taniuchi 1971). We observed clear and severe mating scars on the left pectoral fin of a female (No. Cp-1) in our tank in June 1983. She gave birth to pups in July 1984. In May 1985, 10 months later, we noticed a male pursuing her eagerly and mating scars on her head and left pectoral fin. She gave birth for the second time in June 1986. Although we did not observe mating directly, we assume a gestation period of about 13 months (time from observation of mating scars to birth, Table 16).

Breeding Seasons in Captivity

All the species born or hatched in captivity at the OEA show some seasonality in birth and hatching except for *Scyliorhinus torazame*, which reportedly spawns and hatches in all seasons in the wild (Nakaya 1979) and did so in captivity at the OEA. Hatching and birth occur from April to November when the water temperature in the Kuroshio tank ranges from 22.8°C to 24.9°C, which is almost the same as in the Coral Sea tank (Fig. 16, Table 5). Only data on the breeding seasons of elasmobranchs in captivity is reported here.

The present status of captive elasmobranchs seems to be about the same as it is for cetaceans, i.e., their survival time is generally short in our tanks. Just keeping them in good condition for a long time itself is not easy, to say nothing of breeding them. We believe, however, that if we can make sufficient and suitable facilities to catch, transport, and keep them, and prepare proper conditions and foods for them, and if, moreover, there is a concerned enthusiasm on the part of elasmobranch keepers, then it will not be so difficult to improve this situation in the near future.

Acknowledgments

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Telemetry Studies of Sharks: A Review, with Applications in Resource Management

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ABSTRACT

Ultrasonic telemetry is being increasingly used to study movement patterns and other phenomena in free-ranging aquatic animals. Telemetry studies of sharks are discussed, with examples from pelagic, reef/inshore, and deep-sea environments. Studies are tabulated for 24 species of sharks from 11 families, with the blue shark having the most trackings (58). Other species with substantial numbers of trackings include the gray reef, scalloped hammerhead, lemon, angel, and horn. Most studies have provided basic information on diel patterns of shark movements and space utilization. Trackings using sensor-equipped transmitters also provided data on depth excursions, water and body temperatures, swimming speeds, and other correlates of behavior or physiology.

Suggested uses of telemetry in the practice and management of shark fisheries include determining short- and long-term movements, grouping/schooling habits, small-scale behaviors, and responses to stimuli such as fishing gear. Telemetry also facilitates relocation of animals for direct observations or for capture of specific individuals for age and growth studies.

The technology of telemetry is discussed with regard to transmitter characteristics (size, life, range), attachment and recovery, telemetry of sensor data, and manual vs. automated tracking. Methods of horizontal tracking include ordinary manual (simplest), auto-directional (facilitates tracking), range-measuring (accurate range), X–Y hyperbolic (detailed, real-time plots), and unmanned monitoring (long-term, continuous).

Introduction

The potential of ultrasonic telemetry as a tool for the study of marine fishery resources, including sharks and other elasmobranchs, is just beginning to be realized. Since the first 4-hour tracking of a transmitter-equipped shark (Bass and Rascovich 1965), numerous studies have involved telemetry tracking of sharks (Table 1), although few have yet been reported on skates or rays[1]. While many of these tracking studies were preliminary "first-on-the-species" efforts providing short-term data on patterns of movement, they clearly indicate the potential of the technique for more comprehensive research efforts.

In the broad sense, sharks are regarded as positive resources not only as the target of 1) commercial fisheries for food, oil, leather, etc., but as recreational resources in terms of 2) sport fisheries (Casey and Hoey 1985), 3) public aquarium displays, and 4) underwater activities such as diver tourism and photography. Sharks also represent negative resources in terms of attacks on humans and interference with commercial fishing, research, and military operations (Nelson 1983). Management of sharks from either standpoint requires collection of information about the biology and habits of the species. Biotelemetry is one technique that has been increasingly used for this purpose to study subject animals in the natural environment.

The purpose of this paper is to review previous telemetry studies on sharks, to discuss pertinent technical aspects, and to suggest applications for the use of telemetry in the utilization and management of shark fishery resources.

Previous Studies

As shown in Table 1, at least 31 shark-telemetry studies have been reported, encompassing 24 species of sharks.

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[1] Batoids tracked include cownose rays, *Rhinoptera bonasus* (Blaylock 1988); southern stingrays, *Dasyatis americana* (Snelson et al. 1988); bat rays, *Myliobatis californicus*, and shovelnose guitarfish, *Rhinobatos productus* (Dubsky 1974); and Pacific electric rays, *Torpedo californica* (Lowe et al. 1989).

Table 1.
Summary of telemetric studies of free-ranging sharks.

Family species	Common name	No. individuals tracked	Maximum duration (h, d; C, I)[a]	Author(s)
Alopidae				
Alopias vulpinus	thresher	1	18hC	Dubsky 1974
Carcharhinidae				
Carcharhinus amblyrhynchos	gray reef	26	50hC, 23dI	McKibben and Nelson 1986
		9	72hC	Nelson and Johnson 1980 Johnson 1978
C. leucas	bull	4 +	11dI[b]	Thorson 1971
C. limbatus	blacktip	2	43hC	Nelson and Johnson 1980 Johnson 1978
C. melanopterus	blacktip reef	1	42hC	Nelson and Johnson 1980 Johnson 1978
C. obscurus	dusky	10	13hC	Huish and Benedict 1977
		1	6hC	Carey and Lawson 1973
C. plumbeus	sandbar	3	11hC	Medved and Marshall 1983
C. signatus	night	1	—	Gruber (unpubl. data)
Carcharhinus sp.	(probably sandbar)	1	4hC	Bass and Rascovich 1965
Galeocerdo cuvier	tiger	1	48hC	Tricas et al. 1981
		1	—[b]	Morrissey et al. 1987
Negaprion brevirostris	lemon	9	101hC, 8dI	Gruber et al. 1986, 1988 Gruber 1982
		2	—[b]	Morrissey et al. 1987
Prionace glauca	blue	22	136hC	Carey and Scharold 1987, In press Carey and Gibson 1987 Scharold and Carey 1987, 1986
		18	12hC	Landesman 1984
		4	22hC	Tricas 1979
		14	22hC	Sciarrotta and Nelson 1977
Triaenodon obsesus	whitetip reef	5	10dI	Nelson and Johnson 1980 Johnson 1978
Cetorhinidae				
Cetorhinus maximus	basking	1	17dI	Priede 1984
Ginglymostomatidae				
Ginglymostoma cirratum	nurse	10	96hC	Carrier 1985, 1987
Heterondontidae				
Heterondontus francisci	horn	13	24hC, 57dI	Strong 1988, 1989
		3	24hC	Dubsky 1974
Hexanchidae				
Hexanchus griseus	sixgill	2	36hC, 4dI	Carey (unpubl. data)
Lamnidae				
Carcharodon carcharias	white	1	83hC	Carey et al. 1982
		2	4hC, 6hI	Tricas and McCosker 1984
		1	31hI	McCosker 1987
		2	—	Klimley 1987
Isurus oxyrinchus	shortfin mako	4	104hC	Carey et al. 1981
Sphyrnidae				
Sphyrna lewini	scalloped hammerhead	18	8dI[b]	Klimley et al. 1988 Klimley and Butler 1988a
		13	14hC, 34hI	Klimley and Nelson 1984
		1	15hC, —	Klimley and Butler 1988b
S. zygaena	smooth hammerhead	1	2hC	Bass and Rascovich 1965
Squalidae				
Centrophorus acus	needle dogfish	2	21hC	Yano and Tanaka 1986
Squatinidae				
Squatina californica	Pacific angel	11	12hC, 90dI	Pittenger 1984
		9	25hC	Standora and Nelson 1977
Triakidae				
Mustelus californicus	gray smoothhound	2	20hC	Dubsky 1974
Triakis semifasciata	leopard	6	24hC	Dubsky 1974

[a] Hours (h) or days (d); for continuous/nearly continuous (C) or intermittent (I) trackings.
[b] Using unmanned data-logging monitors.

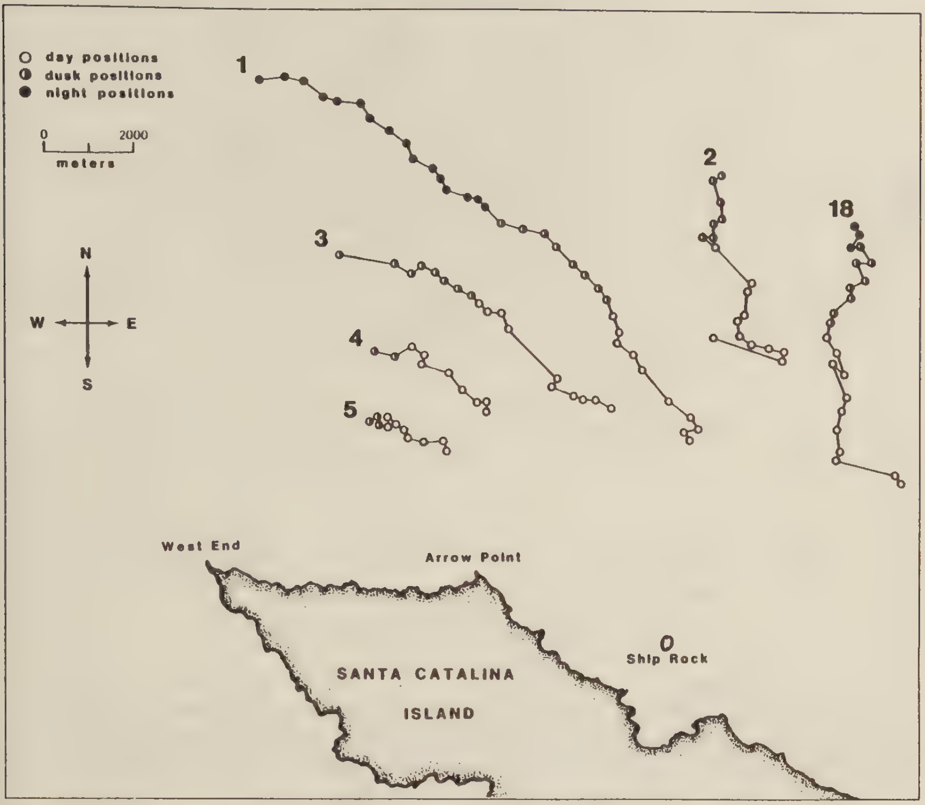

Figure 1.
Horizontal movements of blue sharks tracked during the summer seasons of 1980 (tracks 1, 2, 3, 4, and 5) and 1981 (track 18). Net moves were in the NW quadrant, heading up the mainland California coast. Tracks 2, 3, 4, and 5 are displaced on diagram to avoid overlap (all started near starting point of track 1) but correct directions are maintained. Position points at 15-min intervals. (From Landesman 1984.)

However, some of these were relatively brief efforts or preliminary reports, and the total number of individuals tracked to date is only about 200. Six species have had more than 10 trackings (with some exceeding 24 hours): the blue (58), gray reef (35), scalloped hammerhead (32), angel (20), horn (16), and lemon (11). The longest continuous tracking was 136 hours (blue shark), while the longest intermittent track was 90 days (angel shark). The use of telemetry as a shark research tool is thus in a relatively early stage, and much unused potential remains to be exploited.

Trackings may be divided into those from **pelagic** (open water) environments, those from **reef and coastal** areas, and those from the **deep sea**. The different environments present different tracking problems. Pelagic species are not home-ranging and must generally be tracked continuously or be lost. Sharks from reef/inshore areas can often be successfully tracked intermittently, depending on the degree to which they are home-ranging vs. nomadic. Thus, a home-ranging species may be recontacted on successive days (or at longer intervals) for multiple short periods of tracking, making studies of long-term patterns more feasible. Sharks at great depths pose special problems, e.g., how to capture the animal and how to reduce the stress involved in bringing it to the surface for transmitter application.

Pelagic Trackings

Of the telemetry studies summarized in Table 1, those on the blue and mako sharks showed entirely pelagic (and nomadic) movements, i.e., with the animals over relatively deep open water and not closely associated with the bottom. As such, they were continuous trackings, the durations of which were determined mainly by the endurance of the vessel and crew, or by loss of contact with the signal. Certain other species such as the white and scalloped hammerhead sharks showed major pelagic moves but also some degree of site attachment. Some of the principal findings of these studies are summarized below.

In the Pacific, Sciarrotta and Nelson (1977) conducted 14 one-day trackings of blue sharks in the pelagic environment near Santa Catalina Island, CA. They reported a seasonal shift in horizontal diel movements which might be related to food availability. Sharks tracked during the spring made an evening-twilight migration from offshore to shallower waters near the island. Landesman (1984) tracked 18 blue sharks in the same area off Catalina Island. A seasonal shift again was seen, with island-oriented movements in the spring and the fall, but with offshore NW-quadrant (up coast) moves occurring in the summer (Fig. 1). These horizontal moves averaged 1.5 km/h (day, 1.3; night, 1.7) and showed a relatively high degree of statistical directionality, indicating the animals were well oriented (cues unknown). In terms of vertical moves, most of the sharks exhibited repetitive deep dives, which occurred more commonly during the day and at dusk than during the night.

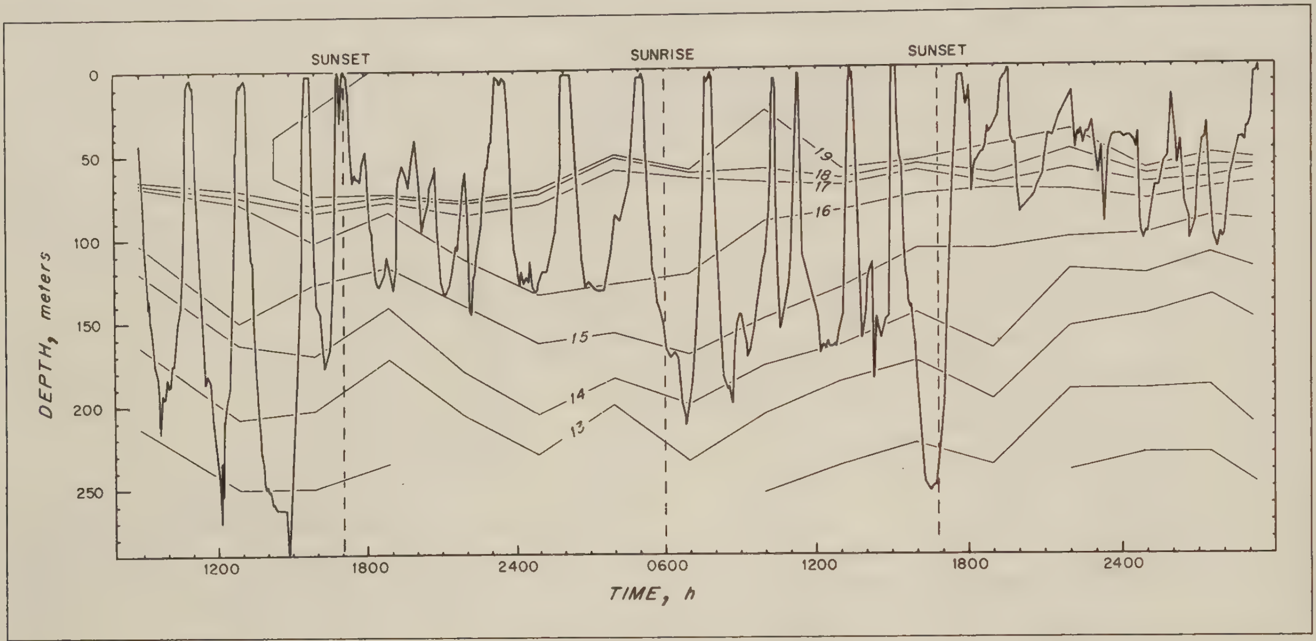

Figure 2.
Telemetered depth record for a blue shark tracked over deep water beyond the continental shelf off the U.S. east coast. Shark's vertical excursions (heavy line) superimposed on a pattern of 1°C isotherms. Repeated dives were of greater amplitude to deeper depths by day than at night. Shark was exposed to temperature changes of many °C. (From Carey and Gibson 1987.)

In the Atlantic, between 1979 and 1986, Carey and coworkers tracked 22 blue sharks, usually for continuous periods of one or more days (Carey and Scharold 1987; in press). They were primarily interested in telemetered sensor data—mainly depth and temperature, but also swimming speed, tailbeat, and heartrate. Some transmitters were multiplexed, with two or more sensors, such as twin-thermistor units, to compare surface and deep-muscle temperatures. Horizontal movements averaged 1.5 km/h (excluding tracks known to be current influenced). Repetitive vertical excursions (Fig. 2) were typical of sharks tracked in deep water, but not of sharks over the continental shelf. A diel component was seen with daytime vertical plunges reaching to deeper depths than those at night. A seasonal variation was also suggested.

Thermal results indicated that, unlike tunas and Lamnid sharks, the blue shark is not warm bodied. As shown in Figure 3, its muscle cools during descent, warms during ascent, following the water temperature relatively closely (with an inertial lag). However, the muscle warms more rapidly than it cools, a phenomenon attributed to the greater effort (and blood flow) required for upward swimming (Carey and Gibson 1987). To investigate the function of the diving pattern, Scharold and Carey (1986) analyzed angles of descent and ascent (from integrated swimming-speed and depth-change data) and swimming/gliding ratios. They concluded that repetitive diving was more likely a strategy for locating food than for saving energy by the swim-glide progression suggested by Weihs (1973).

Four shortfin mako sharks were tracked off the east coast of North America (Carey 1978; Carey et al. 1981). The sharks carried two separate temperature transmitters, one external and one in the stomach. One 2.4-m mako (with food placed in the stomach) was tracked for 104 h and covered a horizontal distance of 280 km. It moved at 2.5 km/h and made numerous vertical excursions to over 400 m, but only rarely rose above 100 m, possibly avoiding the warmer upper mixed layer. Its stomach temperature was typically 6–8°C warmer than the water (Fig. 3). Depth was inferred from external (water) temperature, by comparison to periodic XBT readings taken from the tracking vessel.

A large (4.6 m) white shark was tracked by Carey et al. (1982) in the New York Bight region, using a package consisting of three seperate transmitters, each operating on a different frequency and telemetering a different variable (depth, water temperature, and muscle temperature). In 3.5 days of tracking, starting at the tagging site where it was feeding on a floating dead whale, the shark moved 190 km at an average speed of 3.2 km/h. It swam generally in the region of the thermocline with brief excursions to the surface and bottom, but no obvious diel horizontal or vertical changes were observed. The shark was warm-bodied, but did not thermoregulate. Using heat-transfer data (and other data), an estimate of metabolism was made that implied one large meal would maintain the shark for over one month.

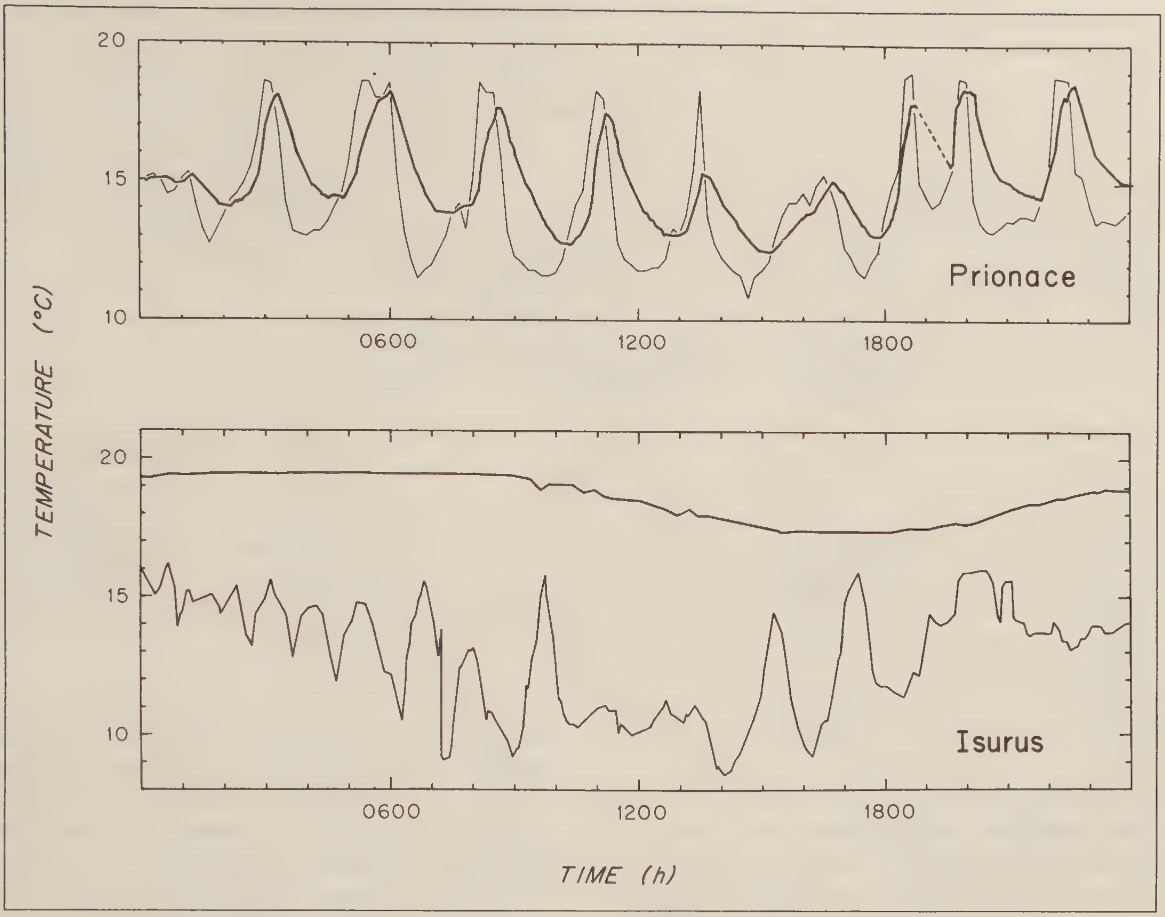

Figure 3.
Internal temperature data from pelagic sharks engaged in repetitive diving behavior. Upper: Telemetered muscle temperature (heavy line) from a blue shark plotted against water temperature obtained indirectly from telemetered depth and bathythermograph data. Lower: Visceral temperature (upper line) of a mako shark from transmitter in stomach, compared with water temperature from externally mounted transmitter. (From Carey and Gibson 1987 [upper] and Carey et al. 1981 [lower].)

Telemetry studies of white sharks in Australia were reported by Tricas and McCosker (1984) and McCosker (1987). In the former study, one shark yielded about 3 hours of muscle-temperature vs. water-temperature data, indicating a warm-bodied condition with the body temperature elevated over ambient by a mean of 3.7°C. The latter study showed that a shark, after ingesting a fish containing a temperature transmitter, elevated its stomach temperature to 7.4°C above ambient. Of interest were two brief stomach-temperature drops which occurred as a result of subsequent bait ingestions. These drops in temperature suggest that such thermal "events" might be useable as indicators of when a telemetered shark feeds.

During studies at the Farallon Islands, CA, Klimley (1987) was able to apply transmitters to two large, bait-attracted white sharks, but contact was lost prematurely. In one case, the signal from an ingested transmitter was greatly weakened—presumably owing to attenuation from fatty pinniped remains in the stomach.

The movements of scalloped hammerhead sharks were studied by Klimley and Nelson (1984) and Klimley et al. (1988) in the vicinity of an offshore seamount in the Gulf of California, Mexico. Normally schooling by day at the seamount, the sharks were tagged with transmitters by free divers using rubber-powered pole spears. Trackings were partly 1) manual, from one or two small boats, and 2) automatic, using bottom-mounted data-logging telemetry monitors. The telemetered sharks generally remained with the large schools during the day, but near dusk departed the seamount (apparently either singly or in small groups) for long excursions into the surrounding pelagic waters, presumably to feed. Many of the sharks returned to the seamount the next morning, and on subsequent mornings after nights away, a pattern which fits the "refuging" system of space utilization described by Hamilton and Watt (1970). Recent work suggests that hammerhead movements may be related to local geomagnetic features (Klimley and Butler

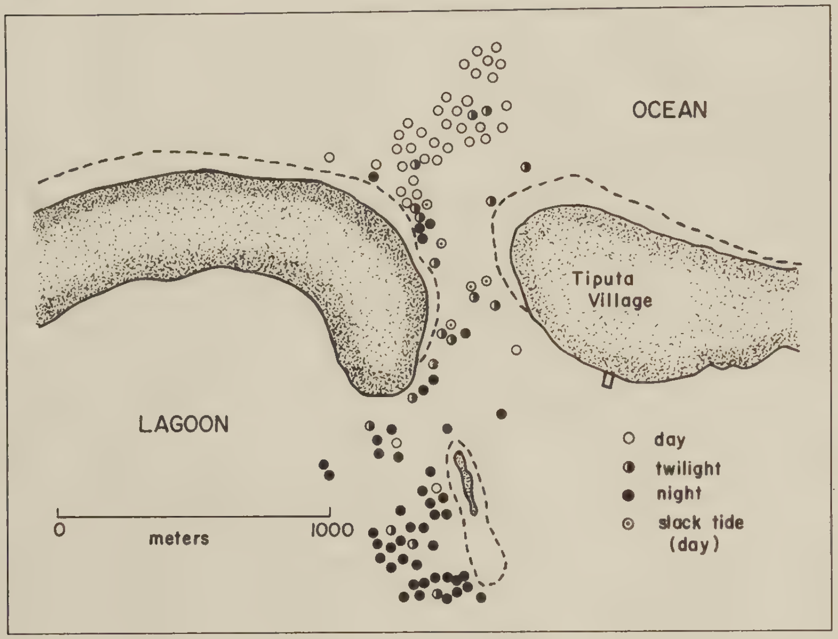

Figure 4.
Horizontal positions of a gray reef shark tracked continuously for 72 hours in the vicinity of Tiputa Pass, Rangiroa Atoll, French Polynesia. Note the distinct separation of day and night areas, and the midpass positions occupied during daytime slack tides. (From the study of Nelson and Johnson [1980].)

1988b) and to water-mass movements (Klimley and Butler 1988a).

A pelagic tracking of special interest was the satellite tracking of a basking shark off Scotland reported by Priede (1984). An *ARGOS*[2] compatible radio transmitter was mounted on a submersible float towed behind the animal (transmitting only while on the surface). An intermittent tracking of 17 days and approximately 120 km was obtained before the tow line broke.

Reef and Inshore Trackings

Many of the reef/inshore sharks are primarily home-ranging in their space utilization behavior, i.e., with substantial overlaps of day-to-day activity spaces. Unlike pelagic species, which are basically nomadic, reef species can, if necessary, be tracked intermittently by relocating the animal anew each day by searching its home-range area. This makes possible long-term telemetry studies on relatively limited resources, using small boats and small tracking crews.

Gray reef sharks, an Indo-Pacific species common around coral atolls, were tracked at Rangiroa, French Polynesia (Johnson 1978; Nelson and Johnson 1980), and at Enewetak, in the Marshall Islands of Micronesia (McKibben and Nelson 1986). The primary method of transmitter application was by ingestion in bait—the unit concealed inside a piece of fish—which caused no initial trauma, but which did result in transmitter regurgitation about three days later. Trackings in the vicinity of the passes at Rangiroa showed quite regular, predictable diel patterns. During the days, the sharks typically milled about in groups in one relatively deep part of their home range. At dusk they moved to another area, usually larger and shallower, presumably for foraging.

Figure 4 shows one gray reef shark tracked continuously for 72 hours in the vicinity of Tiputa Pass, Rangiroa. Its daytime area was deep off the mouth of the pass, whereas it spent its nights actively moving about the shallow reefs at the lagoon end of the pass. The overall activity space for this tracking was 2 km long, 0.83 km^2. A shark from Avatoru Pass did just the opposite, moving from a deep-lagoon daytime area through the pass at dusk to visit shallow ocean reefs at night. At Enewetak, one gray reef shark repeatedly returned by day to a coral pinnacle reef in the center of the lagoon, then roamed widely over the lagoon by night. The daytime activity space (maximum-area polygon) for this shark for the 3-day tracking was 10.3 km^2, while the night space encompassed 28.5 km^2 (53 km^2 overall). At Enewetak, this home-ranging pattern was typical of sharks from the lagoon reefs and pinnacles, whereas sharks of the ocean reef were more nomadic—often making relatively long moves along the perimeter of the atoll, and not returning to the spot where they were originally tagged.

Whitetip reef sharks tracked at Rangiroa showed a strongly home-ranging pattern, moving about mainly at night, and spending large parts of the days resting in specific home caves (Nelson and Johnson 1980).

In the tropical Atlantic in the shallow-water habitat at Bimini, Bahamas, Gruber and coworkers tracked lemon sharks as part of an overall program to study the bioenergetics of this species (Gruber 1982; Gruber at al. 1986,

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[2] Service *ARGOS*, Inc., 1801 McCormick Dr., Suite 10, Landover, Maryland, USA.

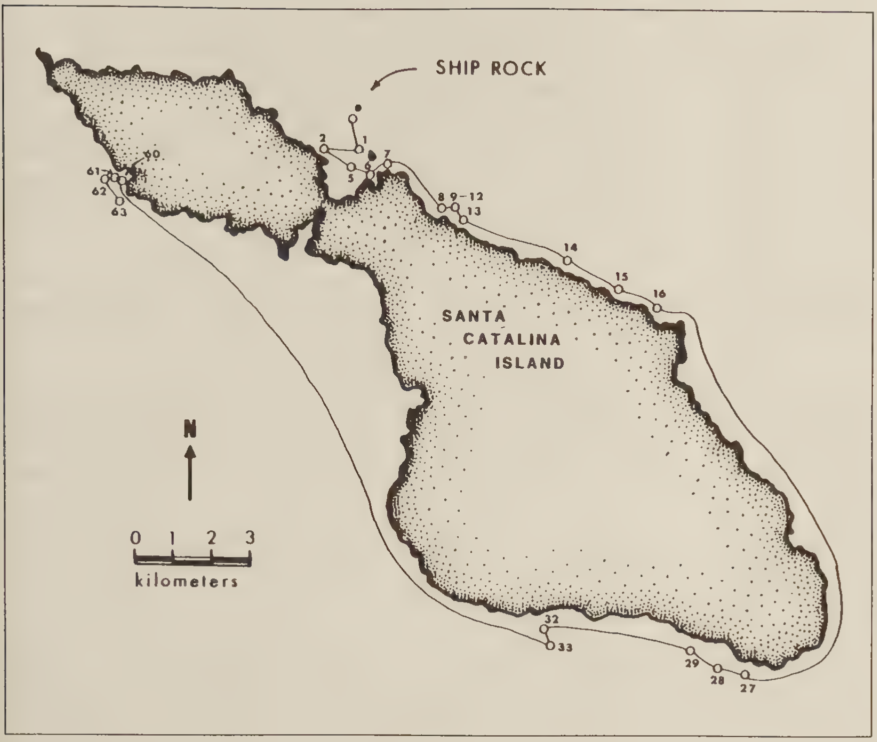

Figure 5.
Two-month intermittent tracking of a Pacific angel shark at Santa Catalina Island, California. Location points show daytime positions, which did not change within a given day. Movements occurred only at night. Numbers indicate the number of days beyond the start of the tracking that the location points were obtained. (From Pittenger 1984.)

1988). In an initial, manual-tracking phase of the project, nine sharks were intermittently tracked for 1 to 8 days; the longest continuous tracking segment lasting 101 hours. All Bimini sharks showed some degree of site attachment, with individual activity spaces from 9 to 93 km^2 (maximum-area polygon). A crepuscular/nocturnal activity peak was observed, and a morning-eastward, afternoon-westward diel pattern occurred that was hypothesized as involving the sun as an orientation cue. The two largest sharks (tracked elsewhere) did not show the above home-ranging pattern, but made long deepwater excursions, suggesting a space-utilization behavior that changes with age. A planned second phase of the Bimini study involved automatic tracking with the aid of data-logging telemetry monitors (Morrissey et al. 1987; Gruber et al. 1986; McKibben et al. 1985).

Using body-cavity implantation, Carrier (1985, 1987) tracked 10 nurse sharks in a shallow bay bordering Big Pine Key, FL. Results indicated a very restricted home area, with movements apparently not correlated to tidal flow. One telemetered shark was recontacted in the same area after a tracking interruption of eight months.

A 4-m tiger shark was tracked continuously for 48 hours at French Frigate Shoals, Hawaiian Islands by Tricas et al. (1981). Captured on longline, the shark was dart-tagged with a depth-sensing transmitter and tracked from a 7-m boat. Horizontally, the shark showed a home-ranging pattern over an area of about 100 km^2, which included shallow reefs, a leeward dropoff, and an epipelagic habitat beyond. During most of the daytime the shark cruised the reef bottom near the dropoff, but at night it moved beyond the reef making repeated vertical excursions to depths of at least 140 m. On both nights the shark then returned to the shallower reefs before dawn.

In temperate waters at Santa Catalina Island, CA, two tracking studies were conducted on Pacific angel sharks. In the initial study (Standora and Nelson 1977), nine sharks were dart-tagged underwater at essentially one spot, Ship Rock, and followed for periods of 13–25 hours. The collective activity space was only 1.5 km^2, a value which did not seem surprising considering the demersal (and supposedly sedentary) nature of angel sharks. However, the subsequent study showed that these single-day trackings grossly underestimated the long-term situation. Pittenger (1984) also tagged his sharks underwater at Ship Rock, but tracked them intermittently over periods of up to 3 months. During this time they showed semi-nomadic movements of many km along the island shoreline, some tracks nearly encircling the 75-km perimeter of the island (Fig. 5). Of 11 trackings with a mean duration of 43 days (maximum of 90), the mean distance travelled was 30.3 km. All movements occurred at night and in a relatively narrow band of depths along the steep island shoreline.

Horn sharks, both adult and juvenile, were tracked by Strong (1988, 1989) at Santa Catalina Island using body-cavity-implanted transmitters (in adults). With intermittent contacts up to 57 days, 13 sharks were subject to a regular schedule of all-night trackings and bi-daily fixes. Ground-zero positioning from a rowed boat was used to avoid artifactual movements due to engine noise. A home-ranging pattern occurred with a high degree of day-to-day repetition (site fidelity) over periods of weeks. The active-phase (night) activity space averaged 0.01 km^2, while the daytime resting area was much smaller, frequently a single point (depending on bottom habitat type), and usually did not overlap the nighttime area.

Young carcharhinid sharks of two species were studied in temperate estuarine habitats on the U.S. Atlantic coast. Huish and Benedict (1978) tracked 10 dusky sharks for periods up to 13 hours in the Cape Fear River, NC. During these trackings, the sharks moved away from the tagging site into deeper water, moving generally with the tidal current. Three sandbar sharks were tracked for about 10 hours each in Chincoteague Bay, VA by Medved and Marshall (1983). These sonic tracks, combined with 20 others using only tethered floats, indicated that tidal current is a major factor determining movement direction and that, to a large degree, the sharks appeared to be carried with the current. No day-night effects were observed.

Using both ultrasonic tracking and conventional tagging, Thorson (1971) confirmed that bull sharks traverse, both upstream and downstream, the full 175 km length of the Rio San Juan between the Caribbean Sea and Lake Nicaragua. Downstream transit times for three telemetered sharks ranged from 7 to 11 days, as recorded by a system of unmanned receiver monitors.

A thresher shark was tracked by Dubsky (1974) for 17.5 hours, using a "hybrid" tag assembly consisting of a sonic transmitter plus a surface float attached by a line. Normally an offshore or pelagic species when adult, this 11 kg juvenile was tagged and moved entirely within the shallows of Morro Bay, CA.

Deep Sea Trackings

There appear to have been only two telemetry studies to date on true deep-sea sharks, i.e., those which primarily inhabit deep water (below continental shelf) and that rarely if ever come near the surface. Besides the need for the transmitter and sensors to withstand the pressures involved, problems include how to capture the animal, how to reduce the stress to the shark when brought to the surface for transmitter application, and how to manage the difficulty of obtaining good horizontal movement plots when the bearing to the shark has a large vertical component. In contrast, vertical movements are easily obtained from telemetered depth-sensor data.

Yano and Tanaka (1986) tracked two needle dogfish in Suruga Bay, Japan. The animals were captured on hook and line from depths of 500 and 600 m and fitted with a harness holding a depth-sensing transmitter. One shark was successfully tracked for 21 hours, during which it generally followed the 500 m sea-bed contour for about 10 km with vertical excursions of 10 to 50 m off the bottom. Its overall depth range, after initially returning to the bottom, was 220 to 680 m. The signal from the second shark failed to move after it reached the sea bed, and it was concluded that the shark had either died or lost the transmitter.

In the summer of 1987, Carey (unpubl. data) tracked two large sixgill sharks along the deep slope off Bermuda. The sharks were tagged with depth-sensing transmitters after having been brought to the surface on handline. During the 2- and 4-day intermittent trackings, the sharks ranged in depth from 550 m to 1500 m and appeared to be on or near the bottom most of the time. They moved horizontally over a distance of 10–14 km, usually remaining near the 700-m bottom contour. An attempt to tag a sixgill at depth from a manned submersible failed owing to the malfunction of an externally mounted speargun.

Summary of Shark-Telemetry Results

1—Sharks, in general, have proven amenable to field study by ultrasonic telemetry. Valid information obtained has included patterns of movement and space use, responses to environmental factors, internal thermal physiology, and telemetry-facilitated direct observations of behaviors such as schooling. However, tagging-induced artifactual behaviors do sometimes occur, e.g., the initial deep dive of harpoon-tagged blue sharks.

2—Horizontally, sharks are relatively wide ranging, with daily activity spaces of km^2 to tens of km^2 for medium to large species. Reef/inshore species typically show a home-ranging pattern, sometimes with a high degree of site fidelity, but also sometimes with a semi-nomadic component in longer-term trackings. Pelagic species show a nomadic pattern, but often with a significant degree of directedness implying orientation to cues presently unknown.

3—Vertically, the repeated up and down swimming pattern of epipelagic sharks appears to be characteristic, and is most likely related to food finding. The occurrence and extent of this behavior is related to location, the diel cycle, and possibly season.

4—Clear, often dramatic, changes occur regularly in phase with the day/night cycle in both reef/inshore and pelagic sharks. Examples include major location shifts, changes in swimming speed and direction, changes in depth or in extent of repetitive diving. Most species show a nocturnal or crepuscular/nocturnal activity peak. Such diel changes are to be expected, and their absence (in a multiday tracking) could suggest a stressed animal not behaving normally. An exception may be sharks from the deep sea, where the diel light/dark cycle does not occur.

5—Seasonal changes have been seen when comparing different trackings of the same species done at different seasons. No single tracking to date has been long enough to demonstrate major migrations or other seasonal periodicities.

6—Maturity (size) is a factor affecting space utilization, with larger individuals having larger activity spaces, different habitat types, and sometimes different utilization patterns in terms of home-ranging vs. nomadism. Territoriality in the strict sense (defense of area) has not been demonstrated in sharks, telemetered or otherwise.

7—The thermal physiology of telemetered sharks differs markedly between the Lamnids (white, mako), which elevate their internal temperature over ambient, and others such as the blue and dusky which do not. Unlike some warm-bodied fishes. e.g., bluefin tuna, sharks have shown no evidence of physiological thermoregulation. Telemetered thermal data (and swimming-speed data) have also been used in estimates of metabolic rate and maintenance diet.

8—Other events not yet telemetered from free-ranging sharks (but possible with appropriate telemetry systems) include food ingestion, finescale movement patterns, large-scale seasonal migrations, and internal physiological processes such as blood flow and stomach secretion.

Technical Considerations

Comprehensive reviews of aquatic telemetering methods and instrumentation include Stasko and Pincock (1977); Ireland and Kanwisher (1978); Mitson (1978); Nelson (1978); Harden Jones and Arnold (1982); Hawkins and Urquhart (1983); and Mohus and Holand (1983). Tracking/positioning methods for ultrasonic telemetry are discussed by Nelson (1987). Radio tracking and telemetry methods for terrestrial wildlife are covered by Kenward (1987). The more general biotelemetry compendia of Amlaner and MacDonald (1980) and Amlaner (1989) contain many useful articles.

Acoustic vs. Radio Telemetry

Telemetry from a shark or other animal submerged in sea water must use **acoustic** signals, as radio waves do not propagate sufficiently in such a conducting medium (at the frequencies used in biotelemetry). Radio tags are often used to track fish in shallow fresh water (Stasko and Pincock 1977), but any **through-the-water** telemetry from fish in the sea must be by acoustic transmission. Furthermore only **ultrasonic** frequencies are used, owing to the resonant characteristics of the relatively small ceramic output transducers used in fish-tracking transmitters.

Any aircraft or satellite tracking, however, must use **radio** signals for the through-air link. Thus, radio techniques can play a role in a marine fisheries study, e.g., the basking shark tracked by satellite (Priede 1984). Timed-release, floating radio tags (Nelson and McKibben 1981) have significant potential for point-to-point trackings of wide-ranging species. Set to release and float up at a specific time, the signal from the floating transmitter can then be detected at relatively long range from shipboard, hilltop, aircraft, or satellite. The *ARGOS* satellite positioning system can determine the location of the transmitter anywhere on the surface of the Earth.

Radio links are also useful for remote ultrasonic receiving systems, e.g., the 3-hydrophone, X-Y positioning system described by McKibben and Nelson (1981). Single radio-relay stations can be used to check on the presence/absence of telemetered animals at a given site.

Transmitter Tradeoffs: Size, Life, Range

The "ideal" sonic tag of minimum size, maximum range, and maximum life is inherently impossible, for the three factors are interdependent and to emphasize one means to sacrifice the others. One must choose which characteristic is most important for the research to be conducted, and make the design trade-offs on that basis. For example, if long life is desired, then output power (and range) must be reduced unless a larger battery can be tolerated. Factors affecting transmitter performance, including through-water propagation of the acoustic signal, are discussed in greater detail by Nelson (1978), Stasko and Pincock (1977), and Brumbaugh (1980).

The life of a transmitter is a function of the power consumption of both 1) the power output stage and 2) the logic circuitry including the crystal oscillator. Other circuits such as sensors or transpond receivers also add to the overall power drain. Normally the logic circuit draws very little power and the major drain is the power stage. One may increase the life of a transmitter by reducing the power duty cycle (percentage of time the power output stage is on) by making the output pulses shorter or the pulse rate slower. If carried too far, however, both of these strategies make tracking more difficult. Pulse rates much slower than 1/s become difficult to track by ear, especially against backgound noise such as crustacean clicks. Short pulses are more difficult to recognize in noise than long pulses because they sound more like clicks than tones. Recognition by ear then requires the reception of a series of pulses at the expected rate. Some automated receiver circuits, however, can reliably recognize single short pulses (McKibben et al. 1985).

Another life-extending strategy is to put the transmitter on a timed on/off cycle controlled by a very low power clock circuit. Thus, the transmitter may be timed to be "on", for example, for 1 h/d, or for 1 wk/mo, etc., and it is only during these times that tracking would be attempted.

Table 2.
Ultrasonic tracking methods for position determination in the horizontal plane. (Adapted from Nelson 1987.)

Tracking method	Transmitter (minimum)	Receiver system	Principle of operation	Advantages	Disadvantages
Ordinary manual					
1 boat	[a]Pinger	Receiver with directional hydrophone	Scan for direction of maximum amplitude	Simplicity, lowest cost	Range estimates relatively poor
1 boat (ground-zero)	Pinger	Same	Maneuver boat until signal vertical	Better accuracy where useable	Close approach may disturb animal
2 boat	Pinger	2 receivers with directional hydrophones	Fix from 2 crossed bearings	Greater accuracy than from one receiver	2 tracking crews at one time
Auto-directional	Pinger	Short-baseline array (2 omnidirectional hydrophones)	Time-of-arrival or phase comparison	Bearing obtained from single pulse	Range estimate poor; custom designed
	Pinger	Cluster of aimed directional hydrophones (2 or more)	Amplitude comparison	Mechanical scanning unnecessary	Range estimate poor; custom designed
Range-measuring					
Timefix	[b]Crystal pinger	Receiver with synchronous clock circuit	One-way arrival time, re: clock pulse	Precise relative range and range changes	Accuracy declines with time; custom
Transpond	[c]Transponder	Receiver with interrogate transmitter	Round-trip arrival time, re: interrogate pulse	Precise, accurate range undiminished with time	Complexity; custom designed
X–Y hyperbolic	Pinger	Long-baseline array (3 omnidirectional hydrophones)	Relative arrival times, fix from crossed time-delay hyperbolae	Accurate pulse-by-pulse plot in real time	Large fixed array, custom designed
Unmanned monitoring	[d]ID-coded pinger	Array of independent data-logging receivers	Reception/verification of contacts; storage of ID codes, times of day	Long-term, continuous monitoring; no behavioral artifacts from tracking	Costly for large array; relative coarse position fixes

[a] Pinger: Simplest ultrasonic transmitter, emits pulses (tone bursts) of a given frequency and a given repetition rate.
[b] Crystal-controlled pinger: Very precise frequency and pulse repetition rate (division of crystal oscillator frequency).
[c] Transponder: Transmitter also containing a receiver circuit, the transpond output pulse triggered by the reception of an interrogate pulse.
[d] ID-coded pinger: Transmitter output coded so that individual units can be distinguished by ear or by automated monitoring equipment. Coding methods include frequency, pulse rate, 2-frequency-doublet interval, and digital frequency-shift keying.

It is therefore possible to circumvent some of the size-life-range limitations which apply to tracking with ordinary transmitters and ordinary receivers. Small, implantable transmitters with good range and with lives of several years are clearly possible, using the appropriate receiving systems. The technology is available, but must be developed for each particular application.

Tracking of Position: Manual vs. Automatic

Most fish tracking studies to date have used what may be termed ''ordinary manual tracking.'' Using one of several commercially available ultrasonic receivers and a directional hydrophone, the tracker rotates the hydrophone—scanning the underwater horizon—to determine the direction to the transmitter. A rough estimate of range is obtained from amplitude of the signal in the earphones. The use of two tracking boats, each with a directional receiver, gives a more accurate crossed-bearing fix. Ground-zero tracking refers to positioning the animal by moving the boat directly above the transmitter. Nelson (1987) discussed these methods, as well as range-measuring (timefix, transponding), automated X–Y, and unmanned monitoring systems in terms of accuracy, precision, and scale and term of phenomena which can be studied using them. These positioning methods are summarized in Table 2.

In directional receiving systems, a distinction is made between those working on amplitude comparisons and those using time-of-arrival differences. Rotation of a single directional hydrophone[3] achieves an amplitude peak (this can be manual or automated), or the amplitudes of several separate hydrophone elements aimed in different directions can be compared. Several fixed tracking arrays of the latter type have been used for tracking from a moving vessel. These include a 2-element (right, left) bow-mounted system of Bass and Rascovich (1965), and the 4-element (right, left, front, back) array mounted on a V-fin depressor towed at depths up to 50 m (Carey and Gibson 1987). Carey has also used a single, bow-mounted rotatable hydrophone (Carey 1978; Lawson and Carey 1972).

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[3] Some directional hydrophones are constructed of several piezoelectric elements connected together in parallel.

Using time-of-arrival differences (or phase differences), a short-baseline array of 2 separate elements can give an accurate signal direction from a single pulse, as in the system described by McKibben and Nelson (1981). The receiver outputs of a two-hydrophone array may also be fed directly to the human ears for a binaural perception of direction (Carey 1978). A towed long-baseline array can be used for positioning a telemetered animal from a moving boat. A linear 3-hydrophone arrangement gives X–Y positions (neglecting distortion due to depth), equivalent to both direction and distance to the transmitter, but with a right/left ambiguity.

A triangular long-baseline array yields an unambigous X–Y position over most of the area within the triangle and certain areas beyond it (Nelson 1987). Resolution is best in the central region (1 m or better for hydrophone spacings of up to several hundred m), diminishing with increasing distance beyond the triangle. Fixed, computerized systems of this type have been described by Hawkins et al. (1974, 1980); Holand et al. (1974); and McKibben and Nelson (1981). An automated X–Y system allows detailed sec-by-sec position plots of telemetered animals within a relatively limited area. Specific, small-scale movement patterns could be identified by this method, e.g., circling, brief acceleration, or straight-line vs. zig-zag swimming.

Reception by unmanned data-logging monitors is well suited to many fishery telemetry applications. At present, this technique is useful for long-term, continuous surveillance at discrete sites, as opposed to short-term, detailed tracking. An array of monitors allows the intermittent "tracking" of many individuals simultaneously without the interference of a tracking boat. A monitor system for detecting and recognizing ID-coded ultrasonic transmitters is described by McKibben et al. (1985) and has been used to study movements of lemon-sharks in Bimini (Gruber et al. 1986; Morrissey et al. 1987) and hammerhead sharks in the Gulf of California (Klimley et al. 1988).

Telemetry of Sensor Data

Simple ultrasonic transmitters without sensors (usually called "pingers") yield only locational information, the accuracy of which is a function of the receiving system. Sensor-equipped transmitters measure one or more variables, such as depth, temperature, light, swimming speed, and compass heading and telemeter this information to the trackers as some modulation on the signal, usually a variation in pulse rate (Stasko and Pincock 1977; Nelson 1978; Mitson and Storeton-West 1985). Multisensor transmitters typically separate the channels by using different frequencies (Lawson and Carey 1972) or by some form of time-multiplexing on one frequency, with demultiplexing of the data done by hand or automatically by computer (Nelson 1978; Cigas and Klimley 1987; Carey and Scharold, In press). In some cases it is possible to infer more than one parameter from a single-sensor transmitter, e.g., depth inferred from temperature and dive angle inferred from swimming speed and rate-of-change of depth (Carey and Scharold 1987; Scharold and Carey 1986).

While the additional data received are valuable, the incorporation of sensors involves tradeoffs. Compared to simple pingers, sensor transmitters are usually larger, more costly, and consume more power. The added cost and reduced transmitter life may not be a problem in the case of tracking a pelagic shark for several days from a large vessel—the transmitter cost still being a relatively small part of the whole tracking operation. However, if the objective is long-term monitoring of numerous individuals, then both the cost and the reduced transmitter life may present a problem.

Transmitter Attachment and Recovery

A variety of methods have been used to attach transmitters to sharks (Table 3). Factors affecting the method of choice include ease of capturing or bait-attracting the shark, size of the shark, fragility of the shark, length of transmitter retention desired, and whether transmitter recovery is desired.

One choice is between atraumatic application (with "normal" behavior from the start of the tracking) and application for long-term retention. Ingestion in bait is atraumatic, but results in the transmitter being regurgitated relatively soon, e.g., about 2–4 days for gray reef sharks (McKibben and Nelson 1986). To prevent regurgitation, McCosker (1987) attached fish hooks to a transmitter fed in bait to a white shark. Harpoon application via barbed dart to a free-swimming individual sometimes results in post-tagging artifacts, e.g., in blue sharks, an initial deep dive (Sciarrotta and Nelson 1977), and, in hammerhead sharks, an immediate rapid departure from sight. There is no data on long-term retention of dart-attached units, but it is probable that they are eventually shed because of tugging by the transmitter on the attachment point. Longest retention will be by internal implantation in the body cavity, but this requires capture and surgery from which some recovery is necessary. The tradeoff here is between (A), initial capture/surgery trauma, and (B), long-term continuous trauma, as from irritation or eroding of the skin at the dart attachment. External dart application may be less serious in terms of (A) but more significant for (B). Internal implantation will have greater (A) but, after healing, probably much less (B) and therefore be better for long-term studies.

Table 3.
Transmitter application methods used in shark-telemetry studies. References for the species tracked are given in Table 1.

Capture status	Application method	Species (examples
Uncaptured	Ingestion in bait	Gray reef, blacktip, blacktip reef, whitetip reef, lemon, white
	Harpoon dart from boat	
	Baited	Blue, white
	Unbaited	Basking
	Harpoon dart underwater	
	Free diving	Scalloped hammerhead
	Scuba	Angel
	Scuba in cage	White
	Submersible	Sixgill[a]
Captured	External 1-point attachment	
	Harpoon dart	Blue, mako, sixgill, dusky, sandbar, tiger
	Fish hook	Sandbar
	Steel pin	Dusky
	External 2-point attachment	
	Dual harpoon darts	Smooth hammerhead
	Darts into skin	Lemon, angel
	Drill through spines	Horn
	Discs, through fin	Bull
	External harness	Needle dogfish
	Internal, stomach (force fed)	Mako, lemon
	Internal, body cavity	Lemon, gray reef, horn, dusky, nurse

[a] Unsuccessful attempt.

Another question is whether to plan for transmitter recovery and reuse. Again, tradeoffs must be considered; a timed-releasable unit is more complex and costly. In addition, a float must be included if surface recovery is desired. Nelson and McKibben (1981) describe release-timing mechanisms for ultrasonic transmitters, some with radio-equipped floats to aid in recovery at sea. For short-term, shallow-water trackings, one may use ingestion in bait and then recover the regurgitated unit from the bottom.

Recovery is necessary if the transmitter package on the shark contains a data-storage unit for recording certain data rather than telemetering it through the water. While such technology has yet to be used on sharks, it is becoming increasingly important in studies of pinniped behavior and physiology, e.g., in recording depths of dives of seals (LeBoeuf et al. 1988). Timed-release transmitters with data-storage circuits are well worth considering for future studies of sharks.

Applications in Fisheries

Developing shark fisheries have historically been difficult to manage against overfishing (Paust and Smith 1986; Anderson 1990), the primary biological reasons being the low growth rates and reproductive potential of elasmobranchs compared to teleosts and the close relationship between recruitment and existing stock size. Bedford (1987) reviewed the history of the emergence, attempted legislative management, and overexploitation of the California pelagic shark fishery, and made a plea for cautious restraint in new shark fisheries until the biological information needed for rational management is obtained.

The major kinds of information traditionally used to make fishery management decisions have not come from telemetry studies, but rather from measurements of the fish catches, as well as from other studies such as conventional tagging. However, with continual advances in the miniaturization and advanced capabilities of telemetry electronics, telemetry holds increasing potential for the kinds of fishery uses discussed below.

The initial use of telemetry has usually been to determine basic patterns of movement and space utilization for the species—habitat preferences, day-night activity spaces, seasonal changes, etc.—to learn **where** the sharks are, and **when** they are there. With more advanced techniques, it is also possible to learn about **what** the animals are doing. These kinds of information are obviously of use to both fishermen and fishery managers.

Short-Term Movements (One to Several Days)

Tracking individuals yields important information on location with respect to diel or tidal phase, and on preference for environmental features such as reefs, seamounts, thermal strata, or oceangraphic fronts. Generally a tracking should be planned to sample one or more full 24-h diel cycles. If not, it should at least cover the transition periods between phases, e.g., the dusk and dawn periods, because these are times when major moves often occur.

The set of position points obtained from the tracking defines an activity space for the animal for that time period. Dimensions can be calculated for this space for comparisons with other trackings, e.g., area by the convex (maximum-area) polygon method (MacDonald et al. 1980). To what degree the pattern is to be called home-ranging or nomadic depends on the amount of overlap of successive daily activity spaces. Thus one needs more than one 24-h day of tracking, preferably several, to determine if a given space represents a "home range".

An example of an interesting horizontal move is the evening-twilight migration of blue sharks from offshore waters to much closer shoreline waters, as determined by one-day (less than 24 hours) trackings (Sciarrotta and Nelson 1977; Landesman 1984). Likewise, the multiday trackings of gray reef sharks uncovered their very regular day-night location changes between the ocean reef and the lagoon (Johnson 1978; Nelson and Johnson 1980). Multiday trackings also showed that lemon sharks display a diel tendency to move westward over shallow flats at night, while returning to deeper waters during the days (Gruber et al. 1988). Knowledge of patterns such as these would, of course, facilitate studying or capturing these animals.

Information on short-term vertical movements is also of interest, especially to fishermen deciding at what depth to set lines or nets. The periodic diving behavior of blue and mako sharks, determined using depth-sensing transmitters, is an example of this (Carey and Scharold, In press; Carey 1978; Landesman 1984). The diel pattern of diving deeper by day, shallower by night appears to be a general one for pelagic sharks and other large species such as swordfish (Carey and Robison 1981) and pinnipeds (LeBoeuf et al. 1988). These changes are likely controlled by light and related to predation on vertically migrating prey, such as those associated with the deep scattering layer.

Trackings can also uncover preferences for certain oceanographic features, such as fronts between horizontally separated water masses of different temperature or productivity, or between vertically separated strata. Ultrasonic trackings of albacore are revealing associations with such features, detected by oceanographic sampling and satellite imagery (Laurs and Brucks 1985; Laurs et al. 1984, 1977). Evidence that hammerhead sharks associate with certain water masses is another example (Klimley and Butler 1988a). Vertical movements of telemetered swordfish appeared more affected by light level and oxygen content than by thermal boundaries (Carey and Robison 1981).

Long-Term Movements (Weeks, Months, Years)

Relatively long-term trackings are needed for uncovering phenomena on a lunar or seasonal scale, such as major migrations, moon-phase effects, or nonperiodic changes such as range expansions. In the past, such questions could only be approached by ordinary (nontelemetric) tagging studies, most of which were hampered by very low tag-recovery percentages. No shark-telemetry study to date has been of sufficient duration to detect such long-term effects. The longest-term shark telemetry work to date—Pittenger's (1984) study of Pacific angel sharks—involved intermittent trackings of up to 90 days. During this time, the 11 individuals made relatively extensive moves (up to 96 km), essentially dispersing themselves around the entire perimeter of Santa Catalina Island. This movement would not have been detected by short-term trackings; indeed the previous study of essentially one-day trackings suggested a very limited home-ranging pattern (Standora and Nelson 1977).

The capability of long-term tracking at reasonable cost is clearly a worthwhile goal for fishery research. As discussed earlier, the transmitter/receiver technology is available (but needs development) for significant improvements in the size and range of transmitters with lives of a year or more. Very long-term studies will almost certainly involve intermittent rather than continuous tracking because of personnel and vessel costs. Unmanned surveillance by data-logging telemetry monitors has real potential for such research. For instance, to study the seasonal migrations of a species, monitors would be placed at intervals along the suspected route or at suspected destinations. Individuals would be tagged with long-life transmitters, and progress along the route would be detected by periodic interrogation of the monitors.

Location of Groupings

Tracking even a single telemetered individual can often lead the trackers to larger concentrations of that species. McKibben and Nelson (1986) followed the signal from a gray reef shark (body-cavity implanted several days before), and it led them to a large polarized school, allowing them to observe and film social behaviors not previously seen. In the Klimley and Nelson (1984) study of hammerhead sharks, one problem was to locate the schools in order to spear-tag the sharks by free diving. Once a transmitter was attached to an individual, it would typically rejoin a school, thus facilitating locating the sharks again for additional tagging. In Pittenger's (1984) long-term trackings of angel sharks, it became evident from the tracking plots that certain locations around Catalina Island were favored daytime spots and that sharks were grouped at these sites.

Knowledge of the precise location of concentrations of a fishery species is obviously of use to both fishermen and to managers. Johnsen (1980) reported a study in which long-term ultrasonic tracking was used to locate the wintering areas of carp in Lake Mendota, Wisconsin. Fish captured and tagged at various spots around the lake eventually moved to two specific aggregating sites. Commercial gill-netters directed to these spots obtained large catches. For various commercial fisheries, the potential exists for the use of pinger-tagging to locate or to maintain contact with concentrations of target species. While harvesting may be facilitated, however, increased vulnerability to overfishing may require altered regulations.

Detection of Small-Scale Behaviors

Besides the relatively large-scale movements of sharks associated with diel or seasonal changes, much could be learned about the animals' behavioral state if much smaller-scale, shorter-term patterns could be detected. Specific behaviors such as brief accelerations, circlings, straight-line swimming, etc. would provide clues to whether the animals are feeding, resting, migrating, and whether grouped or solitary. For example, the telemetered gray reef shark that McKibben and Nelson (1986) observed in a large group was participating in a prolonged circular milling with its conspecifics. This circular pattern (roughly 10-m diameter) could have been detected by certain receiving systems, thereby suggesting the presence of the large group from the behavior of the one individual. Likewise, patterns such as brief accelerations or tight circlings might indicate predatory events, and straight-line swimming might indicate migratory moves (as opposed to foraging).

Ordinary manual tracking is insufficient to resolve these small-scale patterns, the more accurate range-measuring or X–Y positioning being required. For demersal species, a high-resolution system would also indicate whether the animal is motionless on the bottom or moving about in a very limited area. Another way to telemeter small-scale movements is from a compass-heading and/or from swimming-speed sensors in the transmitter package.

Effectiveness of Fishing Gear: Attraction and Repulsion

Telemetry can be used in various experiments to determine effectiveness of fishing methods. In the case of sharks, acoustic attraction might be useful in increasing catch rates of gear such as longlines or gill nets. While the phenomenon of shark attraction to low-frequency, pulsed sounds is well documented (Myrberg 1978; Nelson and Johnson 1972), no specific studies have tested whether sound playback would actually increase catches. Tracking the paths of telemetered sharks could be part of such a study, for instance, to determine maximum distances from which sharks can be attracted.

Repellency behavior can also be studied with telemetry, as in testing whether certain chemical, acoustical, or electrical stimuli would cause avoidance of a given area (Nelson 1983). One fishery concern about sharks is bite damage to gear, e.g., the cod ends of trawls. Electrical devices have been used to repell sharks in this situation (Awbrey et al. 1979). Net-avoidance behavior by the target species could also be studied by telemetry, especially if a high-resolution X–Y system were employed. Detailed movements of telemetered fish as a trawl approaches (the trawl also telemetered) would help assess degree of net evasion.

Facilitation of Direct Observation

It is often useful for the fishery biologist to be able to make direct visual contact with the animals for the purpose of making counts, assessing sizes and sex ratios, or observing reproductive or other behaviors. Underwater viewing can be accomplished by various means, e.g., by free or scuba diving, by manned submersibles, and by remotely operated vehicles (ROVs) or other instrument packages. The problem of locating the animals can be greatly facilitated by telemetry, homing in on the transmitter signal until the individual is sighted. This method has been used in a number of shark studies, in particular those on scalloped hammerheads (Klimley and Nelson 1984) and gray reef sharks (Nelson and Johnson 1980; McKibben and Nelson 1986).

Using a waterproof directional receiver, the diver determines bearing from signal strength. Distance, however, can only be roughly estimated by signal strength, and thus the diver is never certain how close the telemetered animal is. A transponding system, which gives accurate transmitter-to-receiver distance, would be much preferred in this situation, but is more complex. A timefix system using a simple crystal pinger gives only relative (but precise) distance, but does tell the diver if the animal is getting closer or farther away. For conditions or depths unworkable by divers, the use of an ROV to home on and obtain video images of the telemetered animal is technically feasible and of great potential use.

Alternative (or Supplement) to Conventional Tagging

Telemetry tagging is potentially useful for some of the data collection traditionally accomplished by conventional tagging, e.g., for studies of age and growth, population size, migratory and dispersal movements. Ordinary tagging studies are usually characterized by large numbers of individuals tagged, quite low percentage of returns, very irregular return times, and returns often lacking needed information (such as accurate measurements). Yet it is this quantity and quality of data from which the study conclusions must be drawn.

Consider a tagging study in which upwards of 100% of the animals are recovered, and the recoveries are all at the desired times at liberty. With such a body of comparable data, the validity of conclusions would be increased. In the case of age and growth studies of sharks, for instance, individuals given tetracycline injection (Gruber and Stout 1983) could be recovered at the optimum times for interpreting vertebral growth rings. Furthermore, with the research team making the recoveries, all the necessary measurements would be properly taken.

For relatively site-attached species, the above hypothetical age and growth study could be done using small, long-life sonic tags instead of conventional tags. The primary objection would probably be cost. However, while a standard fish tag is far less costly than a transmitter, many fewer transmitters would be needed.

In this example, the cost of recovery of the telemetered sharks must also be considered, as it requires trained personnel with the proper receiving gear. Once the animal is located, there is also the problem of capture. Scuba divers can do this by hand for certain sedentary species such as angel sharks (Pittenger 1984) and horn sharks (Strong 1988). For greater depths, one possibility is an ROV equipped with speargun or net. For active sharks, capturing a specific telemetered individual will be more difficult, but selective hook-and-line fishing would work in some situations. If capture is not necessary, accurate underwater measurements can be made at a distance using the technique of stereophotography (Klimley and Brown 1983).

The sonic-tag approach for tag/recapture research is worth considering for certain limited-ranging, easily-captured species. It would not be feasible for wide-ranging, pelagic sharks such as blue and mako, where recoveries are by chance from scattered sport and commercial fishermen.

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Distribution and Abundance of Skates in the Eastern Bering Sea, Aleutian Islands Region, and the Gulf of Alaska

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ABSTRACT

The distribution, abundance, and relative stock abundance of skate species in the eastern Bering Sea, the Aleutian Islands, and the Gulf of Alaska are examined through the use of information collected from cooperative Japan–U.S. resource assessment surveys. The Fisheries Agency of Japan (JFA) and the National Marine Fisheries Service (NMFS) of the United States have conducted cooperative longline and demersal trawl surveys in the three sea areas since 1979. Survey results indicate that skate species (treated here as a group and denoted as the skate complex) are well distributed and have exhibited stable or increasing trends of abundance throughout the eastern Bering Sea, the Aleutian Islands, and the Gulf of Alaska. The distribution of the Aleutian skate, *Bathyraja aleutica*, in the Gulf of Alaska is also reviewed.

Introduction

Since 1979, the Far Seas Fisheries Research Laboratory (FSFRL), Fisheries Agency of Japan (JFA) has conducted groundfish surveys in cooperation with the Northwest and Alaska Fisheries Center (NWAFC), National Marine Fisheries Service (NMFS), U.S.A., in the eastern Bering Sea, the Aleutian Islands region, and in the Gulf of Alaska. The primary objectives of the surveys have been to obtain current biological information on groundfish and invertebrate resources and to estimate their abundance within the above three sea areas. The results, including biomass estimates (abundance) and other biological parameters obtained through the surveys, are used to assess the stock condition of groundfish resources inhabiting the survey areas. The acceptable catch level is derived for each species based upon these results.

At present, stock assessments are prepared only for species of commercial importance. Biological information for species groups other than those with commercial value has also been accumulated from these surveys. This paper focuses upon one such species group, the skates (which are not being used as a commercially important resource), and will describe their distribution and abundance in the eastern Bering Sea, the Aleutian Islands region, and the Gulf of Alaska. Also, the distribution of the Aleutian skate, *Bathyraja aleutica*, in the Gulf of Alaska is described for the first time.

Materials and Methods

Survey Data

Between 1979 and 1986 two types of groundfish surveys, using bottom trawls and longline gear, were used (under a cooperative agreement) between the North Pacific Groundfish Section, FSFRL, JFA and the Resource Assessment and Conservation Engineering Division, (RACE), NMFS.

Bottom Trawl Surveys—Bottom trawl surveys were conducted every year from 1979 by Japanese research vessels in the areas and months shown in Table 1.

Table 1.

Areas and months where bottom trawl surveys were conducted by Japanese research vessels, 1979–1986. * = Surveys done. EBS = Eastern Bering Sea; AIR = Aleutian Islands region; GOA = Gulf of Alaska.

Year	Areas	May	June	July	August	September	October	November
1979	EBS			*	*			
1980	AIR			*	*	*	*	*
1981	EBS			*	*	*	*	
1982	EBS			*	*	*	*	*
1983	AIR			*	*	*	*	
1984	GOA			*	*	*	*	
1985	EBS	*	*	*	*	*		
1986	AIR	*	*	*	*	*		

The distribution and abundance of skates in the Aleutian Islands in 1983, the Gulf of Alaska in 1984, and the eastern Bering Sea in 1985 were determined using catch data obtained solely by Japanese research vessels. Research vessels chartered by JFA were commercial stern trawlers commonly known as Hokuten trawlers (approximately 349 gross tons). These vessels used large commercial flatfish trawls with a tire and steel bobbin footrope in the Gulf of Alaska and the Aleutian Islands, and a steel bobbin only footrope in the eastern Bering Sea.

Biomass estimates for skate species (all species combined) prior to 1983 in the eastern Bering Sea, the Aleutian Islands, and the Gulf of Alaska were derived from catch data from both Japanese and U.S. research vessels. Analytical results from 1979 through 1982 were published (Bakkala et al. 1985a, b; Sample et al. 1985; Ronholt et al. 1986).

Distribution and abundance patterns of skates in the Aleutian Islands region for 1980, 1983, and 1986 were analyzed using data obtained by both Japanese and U.S. vessels.

Longline Surveys—Japan–U.S. cooperative longline surveys, using the same sampling scheme each year, were conducted annually in the Aleutian Islands region and the Gulf of Alaska between 1979 and 1986 as well as in the eastern Bering Sea between 1982 and 1986. The longline surveys were conducted at depths greater than 100 m and the primary objective of the surveys was obtain biological information on sablefish (*Anoplopoma fimbria*). Details of the sampling methodology and gear used during the surveys are given in Sasaki (1985) (groundline length, hook spacing, hook size, etc.). The eastern Bering Sea was sampled only in the southwestern portion.

Catch data obtained from the longline surveys were used to calculate an abundance index to show the annual change of skate stocks between 1979 and 1986 in the three survey areas. The abundance index reflected the stock status only of skate populations distributed in waters deeper than 100 m.

Analytical Procedures

Since the identification of skates to species is difficult, all species of skates were combined aboard the research vessels and treated as a single group. In this paper, all skate species are considered as a skate complex. However, according to H. Ishihara (10-11-203 Minamifujisawa, Fujisawa, Kanagawa Pref., Japan, pers. commun., Feb. 1988) the three regions are mainly populated by three genera (*Bathyraja*, *Raja*, and *Rhinoraja*).

Bottom Trawl Surveys—In order to determine the distribution pattern of abundance for skates, the catch at each station was standardized into an areal catch rate (kg/km^2) by a relationship between catch (kg) per tow and an area trawled per tow (obtained by the measurement of the horizontal distance between the wing tips of the trawl and the distance trawled). Standing stock (biomass) was estimated using the area-swept extrapolation method of Alverson and Pereyra (1969), i.e., biomass (kg) in a strata was calculated using the mean catch per area trawled by strata (kg/hectre), and the area of the strata. The estimated biomass for the total survey area was obtained by summing the strata biomasses. In deriving the biomass estimate, the vulnerability (ratio of fish caught to fish actually inhabiting the area swept by the trawl) was assumed to be 1.0, i.e., all of the fish in the area trawled were assumed to be caught.

Longline Surveys—Catch data obtained from the longline surveys were processed into relative population weight (RPW) which indicates relative abundance (Sasaki 1985). RPW for a depth zone in a strata is calculated using mean catch per hachi (45 hooks equally spaced along a 100 m groundline) by depth zone (kg/hachi) and is extrapolated to mean catch per area by depth zone. RPW for a strata was obtained by summing the RPW in each depth zone. The RPW for the total survey area is a sum of each strata RPW.

Water Temperature Measurements—Bottom water temperature measurements were obtained using expendable

Table 2.
Biomass estimates (metric tons) for principal species obtained from the 1985 Bering Sea survey.

Species	Biomass[a] (t)	Percentage of total biomass
Walleye pollock	4,633,853	45.3
Yellowfin sole	2,042,417	19.9
Pacific cod	927,714	9.1
Rock sole	734,587	7.1
Alaska plaice	561,599	5.5
Flathead sole	334,024	3.3
Arrowtooth flounder	228,432	2.2
Sculpins	152,409	1.5
Skates	152,256	1.5
Grenadiers	107,624	1.1
Greenland turbot	87,248	0.8
Pacific halibut	68,709	0.7
Sablefish	51,762	0.5
Pacific ocean perch	33,155	0.3
Pacific herring	31,532	0.3
Other flatfish	31,005	0.3
Eelpouts	17,093	0.2
Other rockfish	5,775	0.1
Shortspine thornyheads	5,119	0.1
Other species	17,637	0.2
Total	10,223,950	100.0

[a] From Walters et al. 1988.

Table 3.
Biomass estimates (metric tons) for principal species obtained from the 1983 Aleutian Islands survey.

Species	Biomass[a] (t)	Percentage of total biomass
Walleye pollock	539,380	27.9
Giant grenadier	381,219	19.8
Atka mackerel	306,782	15.9
Pacific ocean perch	144,079	7.5
Pacific cod	136,887	7.1
Sablefish	68,543	3.6
Greenland turbot	49,832	2.6
Northern rockfish	44,458	2.3
Arrowtooth flounder	39,888	2.1
Shortraker rockfish	27,914	1.4
Rougheye rockfish	20,581	1.1
Rock sole	19,316	1.0
Pacific halibut	17,771	0.9
Skates	17,439	0.9
Popeye grenadier	17,106	0.9
Shortspine thornyheads	15,138	0.8
Rex sole	1,746	0.1
Flathead sole	816	<0.1
Dover sole	389	<0.1
Other species	80,567	4.2
Total	1,929,851	100.1

[a] From Wakabayashi et al. 1988.

Table 4.
Biomass estimates (metric tons) for principal species obtained from the 1984 Gulf of Alaska survey (170°W–144°W).

Species	Biomass[a] (t)	Percentage of total biomass
Walleye pollock	1,201,374	23.5
Arrowtooth flounder	1,080,190	21.1
Pacific cod	535,835	10.5
Sablefish	394,842	7.7
Pacific halibut	319,767	6.3
Flathead sole	276,946	5.4
Giant grenadier	250,540	4.9
Pacific ocean perch	174,023	3.4
Skates	134,548	2.6
Rock sole	124,282	2.4
Shortspine thornyhead	77,576	1.5
Yellowfin sole	76,183	1.5
Northern rockfish	75,552	1.5
Rex sole	68,395	1.3
Rougheye rockfish	64,938	1.3
Dover sole	63,074	1.2
Pacific herring	49,369	1.0
Atka mackerel	36,064	0.7
Dusky rockfish	25,707	0.5
Shortraker rockfish	20,715	0.4
Butter sole	18,350	0.4
Starry flounder	15,137	0.3
Coryphaenoides cinereus	10,898	0.2
Myoxocephalus sp.	10,680	0.2
Yellow Irish lords	10,103	0.2
Total	5,115,088	100.0

[a] From Brown 1986.

bathythermographs during the surveys and were analyzed to define their relationship to skate distribution.

Results

Biomass Estimates

Skates comprised less than 3% of the biomass in the eastern Bering Sea, the Aleutian Islands, and the Gulf of Alaska (Tables 2–4). Two or three principal species comprised the majority of the groundfish in each area. Walleye pollock and yellowfin sole accounted for 65% of the groundfish biomass in the eastern Bering Sea (Table 2); walleye pollock, giant grenadier, and Atka mackerel comprised 64% in the Aleutian Islands (Table 3); and walleye pollock, arrowtooth flounder, and Pacific cod accounted for 55% of the total in the Gulf of Alaska (Table 4).

With the exception of these principal species, no other individual species accounted for more than 10% of the total biomass in any area. The skate complex constituted 1.5% of the biomass in the eastern Bering Sea, nearly 1% in the

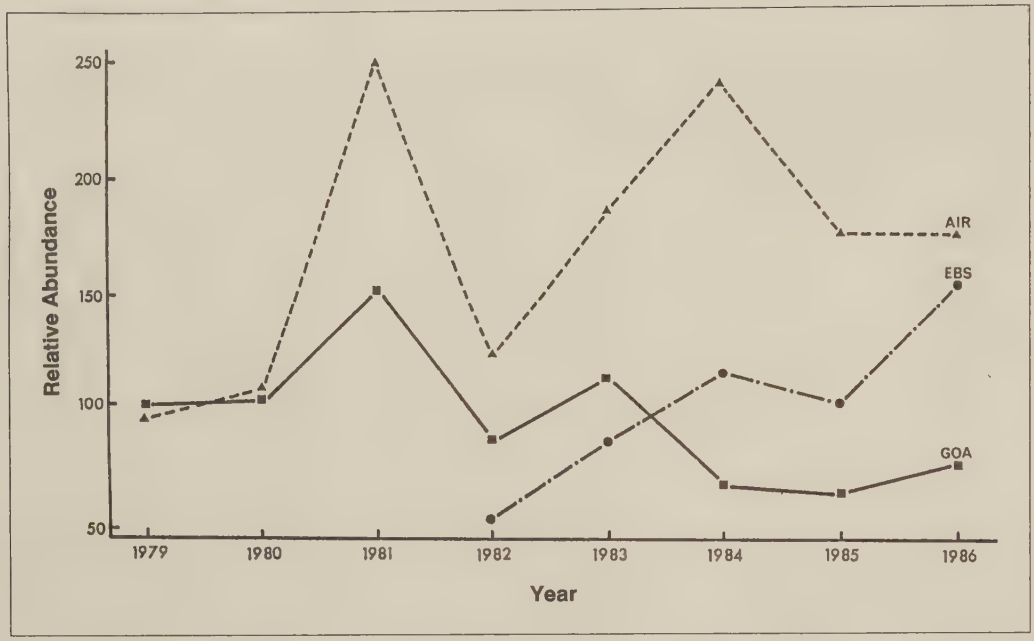

Figure 1.
Annual changes in the relative abundance for skates obtained from Japan–U.S. cooperative longline surveys in the eastern Bering Sea, Aleutian Islands region, and the Gulf of Alaska. AIR = Aleutian Island region, EBS = Eastern Bering Sea, and GOA = Gulf of Alaska.

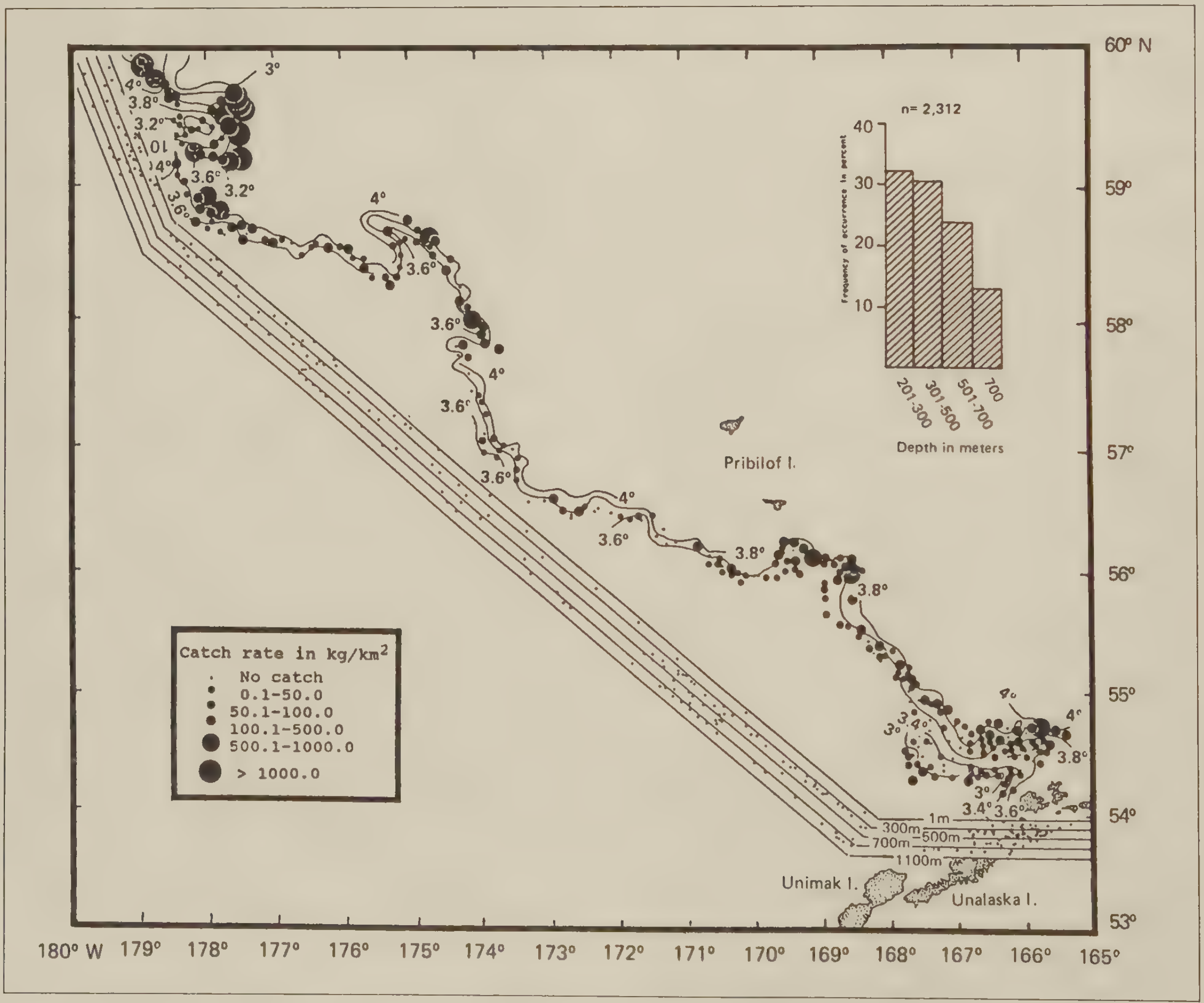
60° N
59°
58°
57°
56°
55°
54°
53°
180° W
179°
178°
177°
176°
175°
174°
173°
172°
171°
170°
169°
168°
167°
166°
165°
n= 2,312
40
30
20
10
Frequency of occurrence in percent
201-300
301-500
501-700
700
Depth in meters
Pribilof I.
Unimak I.
Unalaska I.
1m
300m
500m
700m
1100m
3°
4°
3.8°
3.2°
3.6°
3.4°
Catch rate in kg/km²
No catch
0.1-50.0
50.1-100.0
100.1-500.0
500.1-1000.0
> 1000.0

Figure 2.
Distribution and abundance of the skates in the eastern Bering Sea (slope area) obtained from the 1985 cooperative Japan–U.S. groundfish trawl survey.

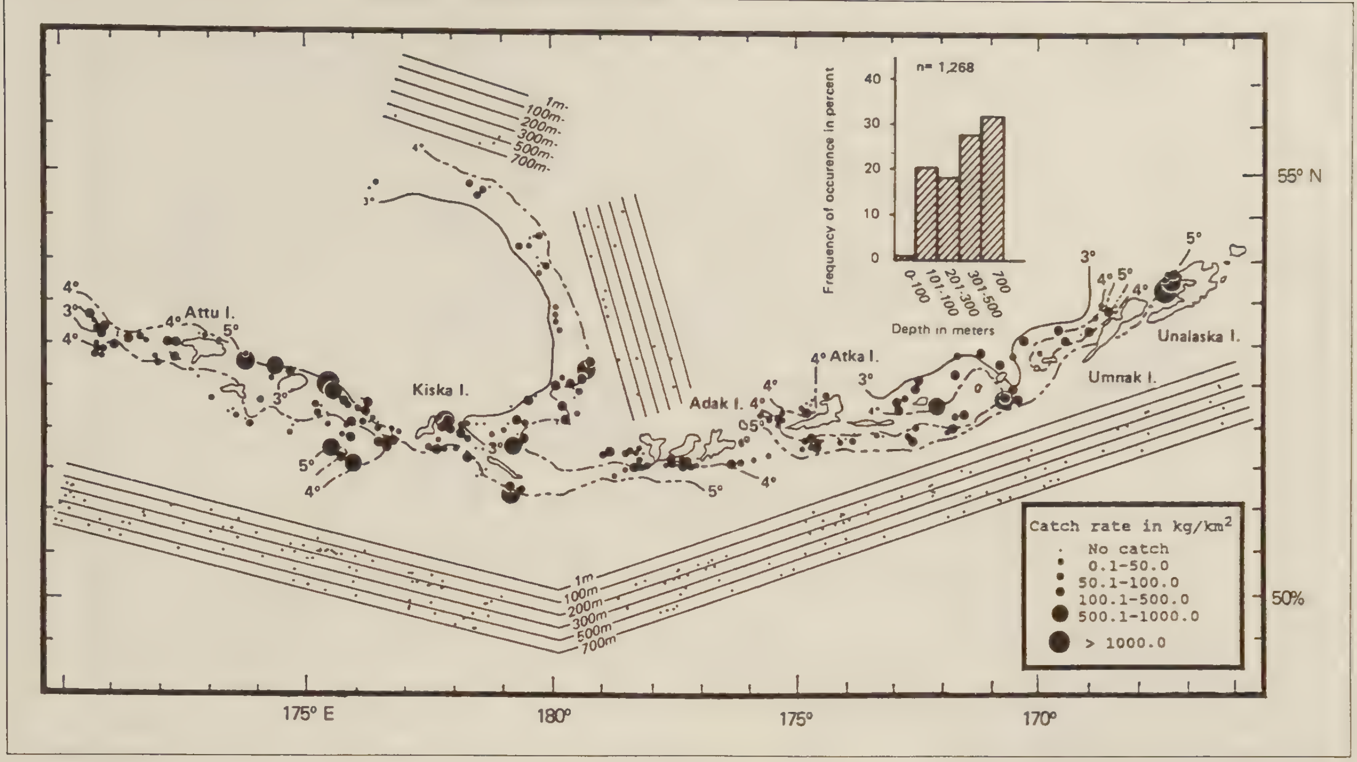

Figure 3.
Distribution and abundance of the skates in the Aleutian Islands region obtained from the 1983 cooperative Japan-U.S. groundfish trawl survey.

Aleutian Islands, and 2.6% in the Gulf of Alaska. Thus the skate complex ranked about midposition in each area in terms of importance of the nonprincipal species or species groups.

The total estimated biomass of the skates species is 304,243 metric tons (t) for the continental shelf and slope of the area sampled by the three surveys.

Annual Changes in Relative Abundance

The time series of cooperative longline surveys (Fig. 1) allows the evaluation of annual changes in the relative abundance of skates. The abundance of skates in the eastern Bering Sea has been increasing since 1982, while in the Gulf of Alaska it has decreased slightly between 1981 and 1986. Relative skate abundance from longline surveys in the Aleutian Islands shows large fluctuations from 1980 to 1984, with a leveling off in 1985 and 1986.

Distribution and Abundance

The distribution and abundance (kg/km^2) of the skate complex for the eastern Bering Sea in 1985, the Aleutian Islands in 1983, and the Gulf of Alaska in 1984 are shown in Figures 2–4. The distribution of the Aleutian skate, *Bathraja aleutica*, in the Gulf of Alaska in 1984 is also shown in Figure 5. The *B. aleutica* distribution is shown only for the continental slope area of the western and central Gulf of Alaska, the area sampled by the Japan chartered Hokuten trawler during the 1984 survey.

Skate distribution was closely associated with the slope area in the eastern Bering Sea (Fig. 2). Dense concentrations were encountered in the northwest and southeast portions of the survey area primarily at depths between 200 and 700 m. Highest densities were found in the area between 59–60°N. Skate abundance tended to decrease with increasing water depth in the Bering Sea.

In the Aleutian Islands region, skates were found to be uniformly distributed throughout the survey area, occurring in nearly equal abundance both north and south of the island chain (Fig. 3). Relatively dense concentrations were encountered in the western Aleutian Islands in the area between Attu Island and long. 179°E and also in the eastern Aleutian Islands in the area northwest of Unalaska Island. Contrary to the eastern Bering Sea results, skate species in the Aleutian Islands show an increasing abundance with increasing water depth.

Skates exhibited a sporadic distribution in the Gulf of Alaska compared to the eastern Bering Sea and the Aleutian Islands (Fig. 4). Although small quantities of skate species appeared at many survey stations, highest densities occurred in the southeastern offshore Kodiak area between

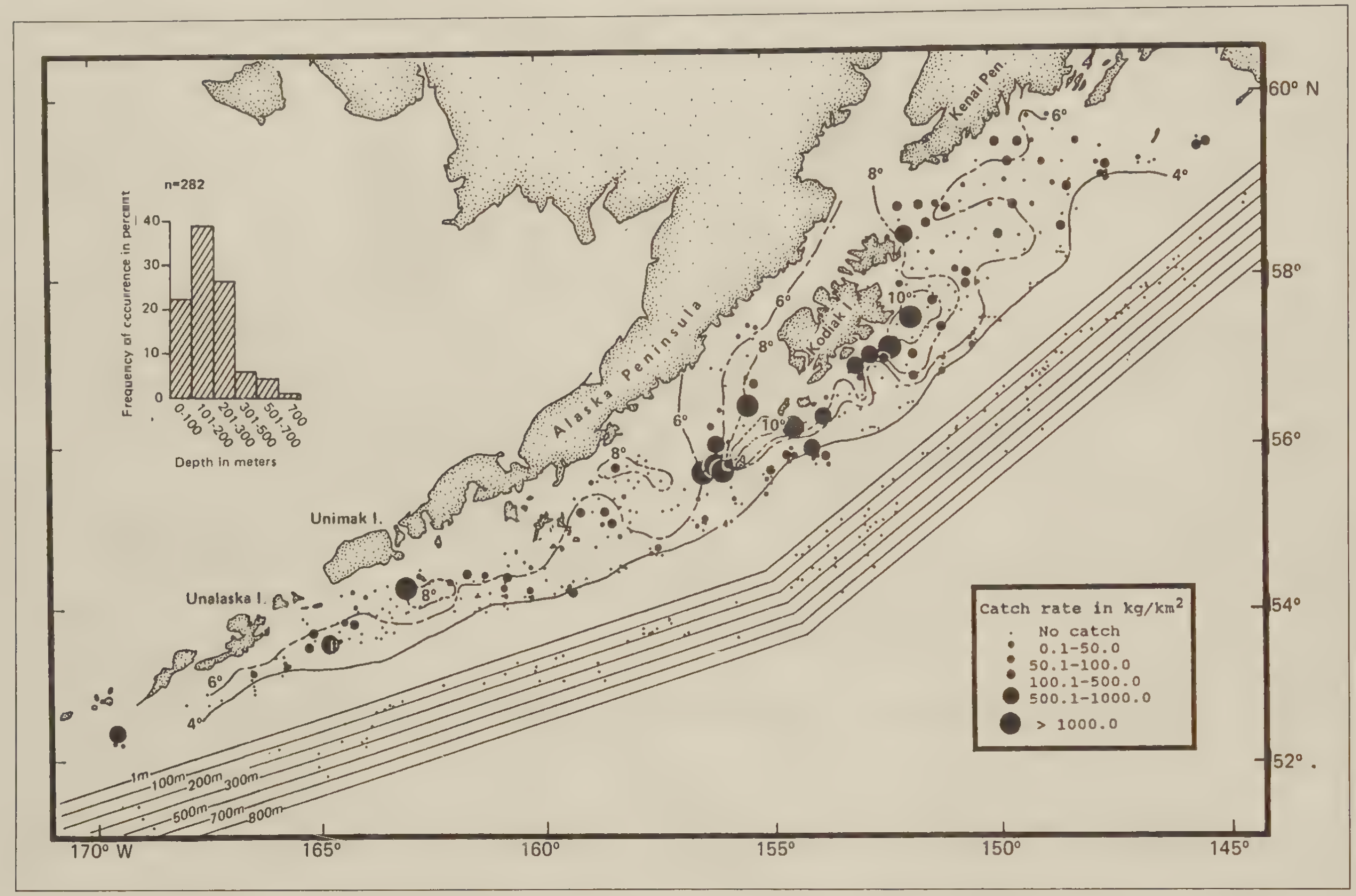
n=282
Frequency of occurrence in percent
40
30
20
10
0
0-100
101-200
201-300
301-500
501-700
700
Depth in meters
Kenai Pen
Alaska Peninsula
Kodiak I.
Unimak I.
Unalaska I.
4°
6°
8°
10°
Catch rate in kg/km²
No catch
0.1-50.0
50.1-100.0
100.1-500.0
500.1-1000.0
> 1000.0
1m
100m
200m
300m
500m
700m
800m
60° N
58°
56°
54°
52°
170° W
165°
160°
155°
150°
145°

Figure 4.
Distribution and abundance of the skates in the Gulf of Alaska obtained from the 1983 cooperative Japan-U.S. groundfish trawl survey.

long. 150–157°W. By depth, the highest abundance of skate species (85%) were distributed in waters less than 300 m.

The Aleutian skate had a widespread, non-uniform distribution in the Gulf of Alaska, characterized by small areas of dense skate aggregations forming localized areas of high abundance (Fig. 5).

Results from triennial bottom trawl surveys in 1980, 1983, and 1986 off the Aleutian Islands also provide a time series of comparative data to ascertain skate distribution and abundance (Figs. 6, 7). To facilitate comparison between surveys, the survey area was divided into four strata at 180 degrees longitude both north and south of the island chain; southwest (170°E–180°, south side); southeast (180°–170°W, south side); northwest (170°E–180°, north side); and northeast (180°–170°W, north side).

A relatively similar distribution pattern was found for skates in the southwest and northwest strata during 1980, 1983, and 1986 and in the southeast and southwest strata between 1980 and 1983. During the 1986 survey high skate abundance was found in the eastern Aleutian areas between 172°–174°W (Amukta and Seguam Passes) and also in the central Aleutians near 180 degrees (Petrel Bank). Biomass estimates from the three Aleutian Islands surveys (Fig. 7) indicate that the skate biomass tended to be slightly higher in the eastern strata (southeast, northeast), than in the western strata (southwest, northwest) and was primarily distributed at depths greater than 100 m.

Species Composition

Seven skate species from two genera were identified from the catch of US vessels participating in the 1980 Aleutian Islands trawl survey (Ronholt et al. 1986). The major species were *Bathyraja rosispinis* (32% of the Rajidae biomass), *B. aleutica* (27%), *B. kincaidi* (20%), *Raja binoculata* (9%), and *R. stellulata* (7%). The two remaining species, *B. abyssicola* and *B. trachura*, contributed only 5% of the total Rajidae biomass.

Water Temperature and Distribution

Results from the three surveys of the eastern Bering Sea slope area (July–October 1981, 1982; May–September 1985) indicate the presence of skates where bottom water temperatures ranged from 3 to 5°C . Particularly notable

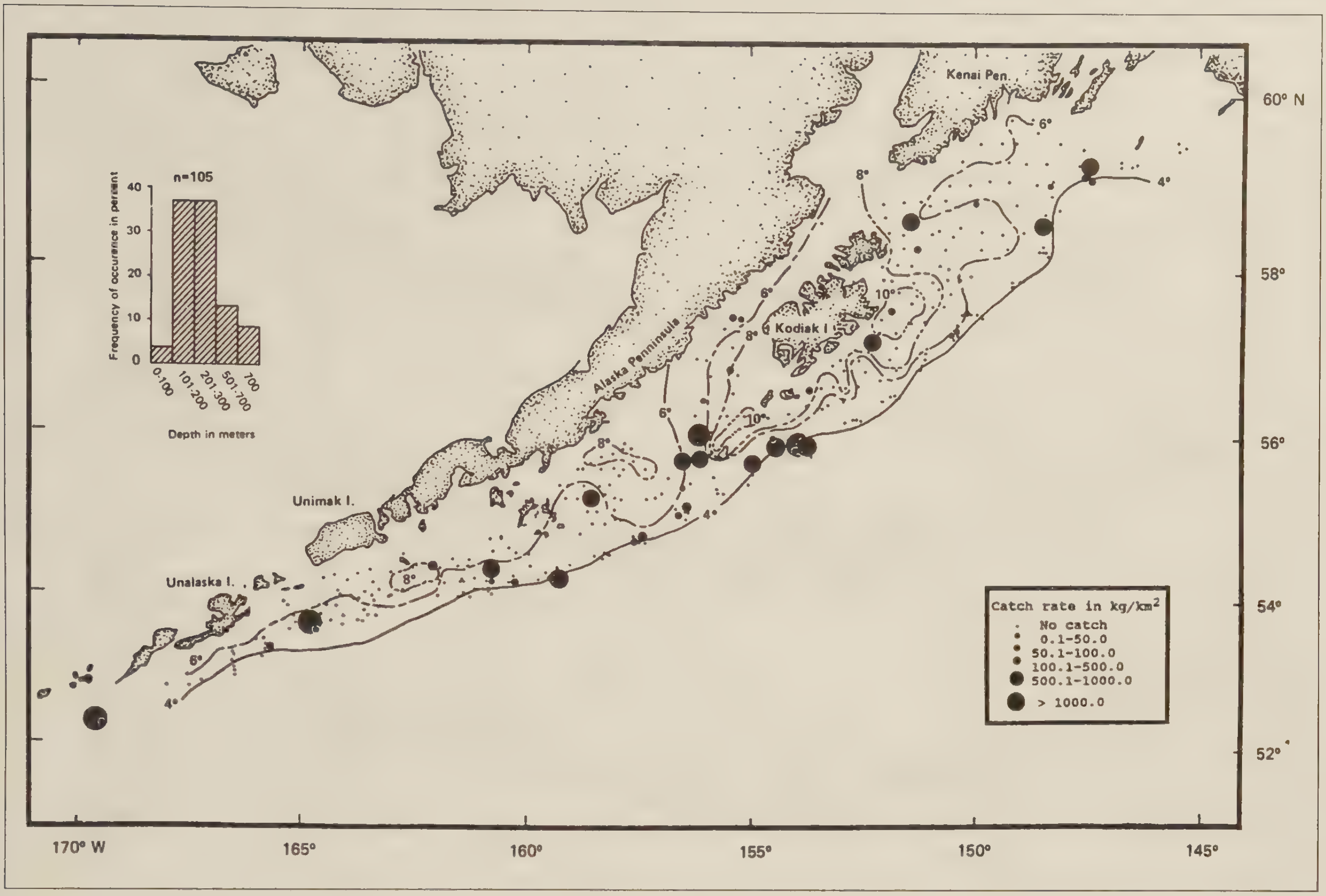
n=105
Frequency of occurence in percent
40
30
20
10
0
0-100
101-200
201-300
501-700
700
Depth in meters
Kenai Pen.
Kodiak I.
Alaska Penninsula
Unimak I.
Unalaska I.
6°
8°
10°
4°
60° N
58°
56°
54°
52°
170° W
165°
160°
155°
150°
145°
Catch rate in kg/km²
· No catch
• 0.1-50.0
• 50.1-100.0
• 100.1-500.0
● 500.1-1000.0
● > 1000.0

Figure 5.
Distribution and abundance of the Aleutian skate, *Bathyraja aleutica* in the Gulf of Alaska obtained from the 1984 cooperative Japan-U.S. groundfish trawl survey.

were the 1985 survey data where skate catches were confined to the 3-4°C isobath.

During the Aleutian Islands trawl survey (July-October 1983) skates were taken from waters where bottom temperatures ranged between 3-6°C. In the Gulf of Alaska (July-October 1984) skates were caught primarily at stations where the bottom temeratures ranged from 4 to 7°C. No conclusive relationship was established between skate abundance and bottom water temperatures from any of the three sea areas.

Discussion

Stock Condition

The estimated biomass for skates inhabiting the eastern Bering Sea increased from 73,800 t in 1979 to 158,000 t in 1981, to 177,200 t in 1982, and decreased to 152,300 t in 1985 (Walters et al. 1987). These trawl survey results indicate that skate abundance has been relatively stable since 1981. Based on catch data from NWAFC trawl surveys (U.S. data only), the biomass estimates for skates in the eastern Bering Sea have increased from 123,100 t in 1980 to 258,000 t in 1986 (Bakkala 1987). This increasing trend is further supported by the relative abundance index available from the eastern Bering Sea longline surveys (Fig. 1).

Biomass estimates of skates in the Aleutian Islands, available from cooperative Japan-U.S. trawl surveys (Ronholt et al. 1986; Wakabayashi et al. 1988) indicate that the resource in this region increased from 10,700 t in 1980 and 17,000 t in 1983 to 19,000 t in 1986. A similar trend is apparent from the U.S. data from the same surveys, which provide estimates of 13,700 t in 1980, 12,100 t in 1983, and 19,100 t in 1986 (Bakkala et al. 1985a, b). The relative abundance index for skates, determined from the cooperative longline surveys, shows large annual fluctuations for the Aleutian Islands in contrast to trawl survey results. The fact that the relative population weight index never dropped below the 1982 value during subsequent survey years supports the notion of stable or perhaps increasing stock abundance for skates developed from the Aleutian Islands trawl survey results.

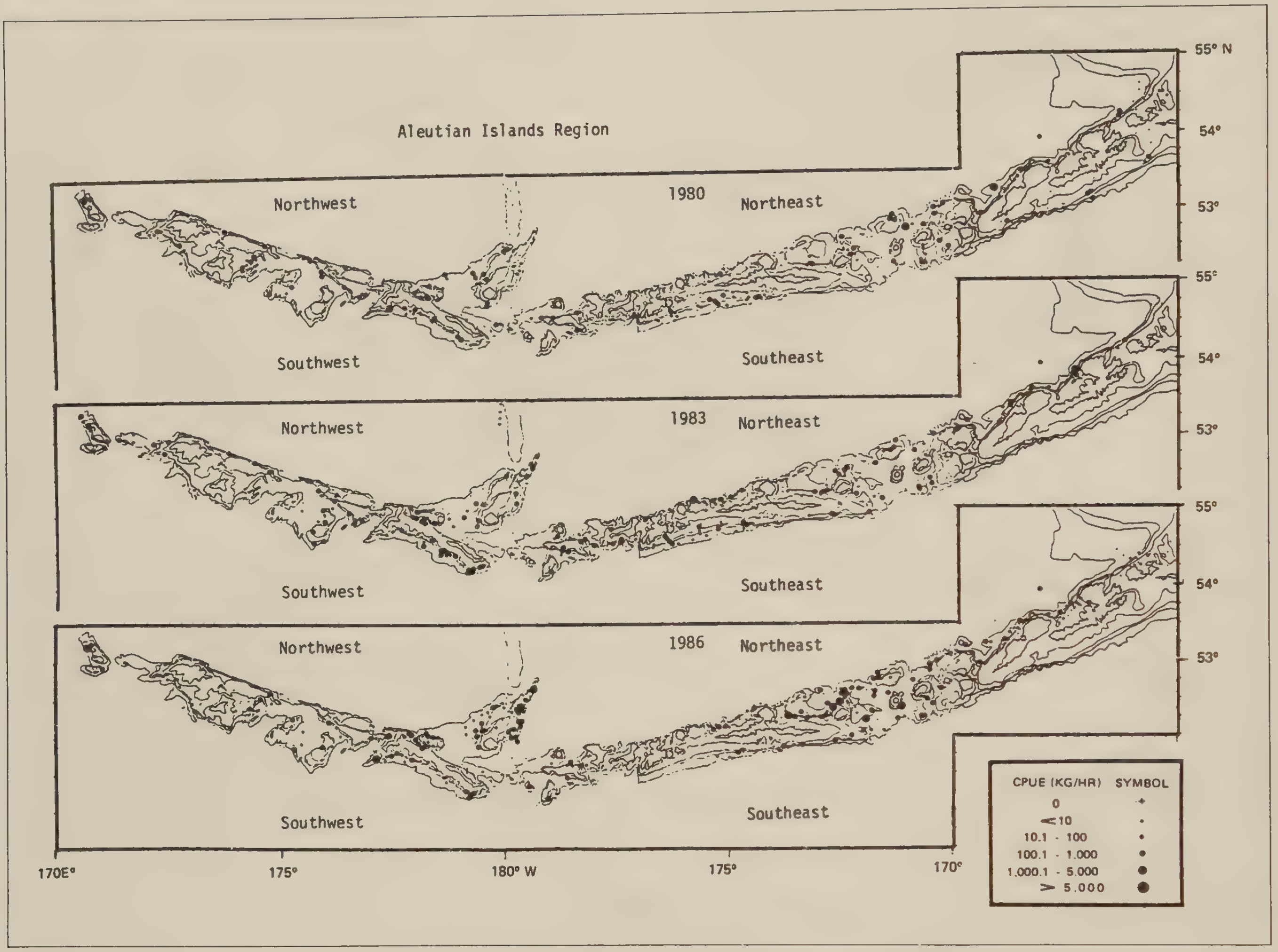
Aleutian Islands Region
1980
Northwest
Northeast
Southwest
Southeast
1983
Northwest
Northeast
Southwest
Southeast
1986
Northwest
Northeast
Southwest
Southeast
55° N
54°
53°
55°
54°
53°
55°
54°
53°
170E°
175°
180° W
175°
170°
CPUE (KG/HR) SYMBOL
0
<10
10.1 - 100
100.1 - 1.000
1.000.1 - 5.000
> 5.000

Figure 6.
Distribution and abundance of the skates in the Aleutian Islands in 1980, 1983, and 1986.

No comparative information is available on absolute skate abundance in the Gulf of Alaska because only a single biomass estimate of 134,500 t resulted from the 1984 cooperative groundfish trawl survey (Brown 1986). However, the time series of comparative relative abundance information from the cooperative longline surveys conducted from 1979 to 1986 in this region is useful to examine abundance trends. As previously mentioned, the cooperative longline surveys were designed primarily to sample the depth distribution of sablefish (100–1,000 m), and because 70% of the Gulf of Alaska skate resource appears to be distributed at depths below 100 m, the assumption is made that the relative abundance index from these surveys should also represent the status of the skate resource. The skate abundance in the Gulf of Alaska has shown a decreasing trend since 1981 (Fig. 1).

Productivity and Distribution Patterns

Biomass estimates for skates in the eastern Bering Sea, the Aleutian Islands, and the Gulf of Alaska are 260,000 t, 19,000 t, and 134,500 t, respectively. The total area surveyed for the three regions was 665,000 km^2, 91,000 km^2, and 257,000 km^2, respectively. The biomass density per unit area approximately 0.4 t/km^2 in the eastern Bering Sea, 0.5 t/km^2 in the Gulf of Alaska, and 0.2 t/km^2 in the Aleutian Islands. Although no individual length-weight measurements were recorded for any skate species to establish growth curves by area, the biomass density/unit area estimates suggests that the productivity of skates in the Aleutian Islands is less than in the eastern Bering Sea or the Gulf of Alaska.

The distribution by depth shows similarities between the eastern Bering Sea and the Gulf of Alaska where skates tend to inhabit shallower areas and most of the biomass occurs at depths less than 500 m. A different depth distribution was found in the Aleutian Islands where over half the skates were distributed at depths greater than 500 m.

One possible explanation for the different depth distributions in the Aleutian Islands may be attributed to the

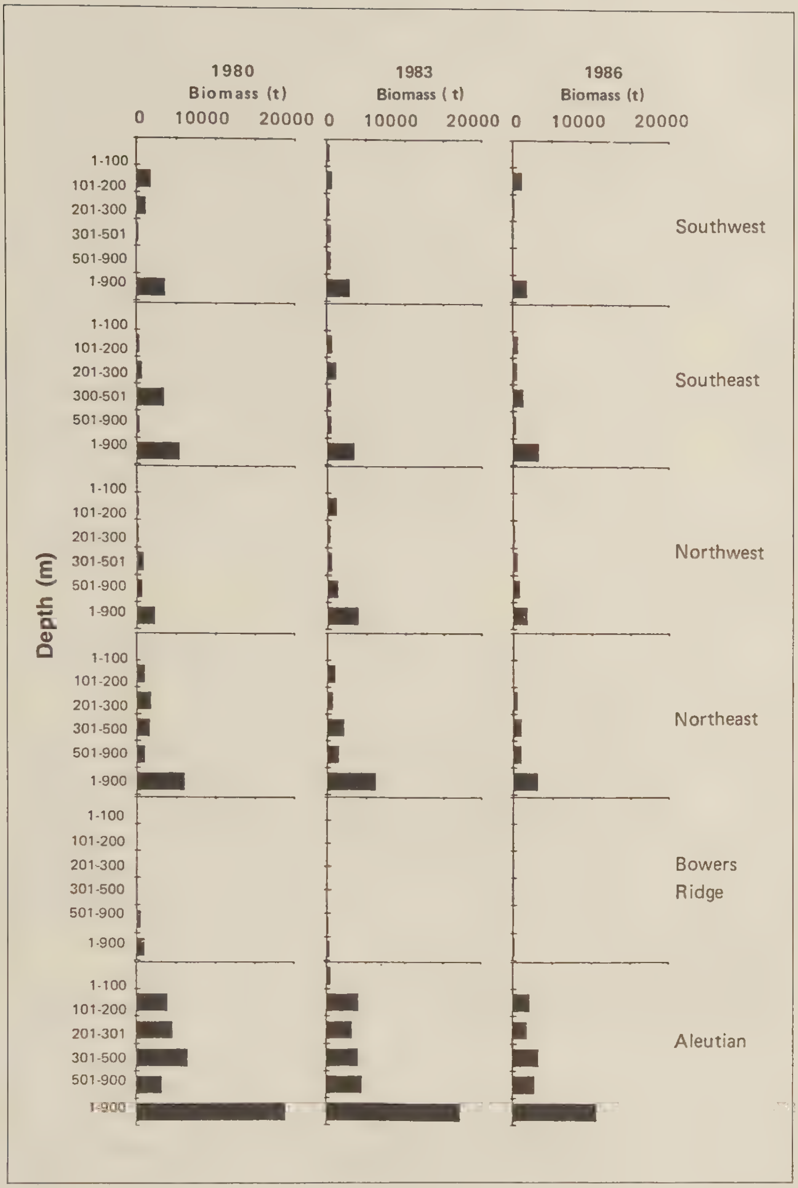

Figure 7.
Estimated biomass of the skates by depth zone in the Aleutian Islands region in 1980, 1983, and 1986.

bathymetry of the island archipelago. This region is characterized by a very narrow continental shelf with steep slope areas. The shelf portion of the survey area comprises 21% of the total survey area compared to 95% in the eastern Bering Sea and 82% from the Gulf of Alaska. This peculiarity of the skate depth distribution in the Aleutian Islands may offer a possible explanation for the lower productivity from this region. If the preferred habitat for skates is the narrow continental shelf, then intraspecific and interspecific competition may force some of the population to inhabit suboptimal habitats (although this is difficult to substantiate without better species identification).

The differences among the skates distributions in the Aleutian Islands during the three survey years may have been a function of the date of the survey. The 1980 and 1983 surveys were conducted from July through October and produced similar distributional patterns. The 1986 survey was conducted from May through September and found relatively larger aggregations of skates in the eastern portion of the survey area.

Relationship of Distribution to Bottom Water Temperatures

Skates were captured at water temperatures between 3 and 4 °C in the eastern Bering Sea slope area (Fig. 8). However, it is difficult to determine the optimal water temperature suitable for skate habitation from the 1985 survey as temperatures of 3 and 4°C were encountered during the entire survey period. The same situation existed during the Aleutian Islands survey in 1983. Restrictive isotherms resulted in inconclusive data for to describing the relation-

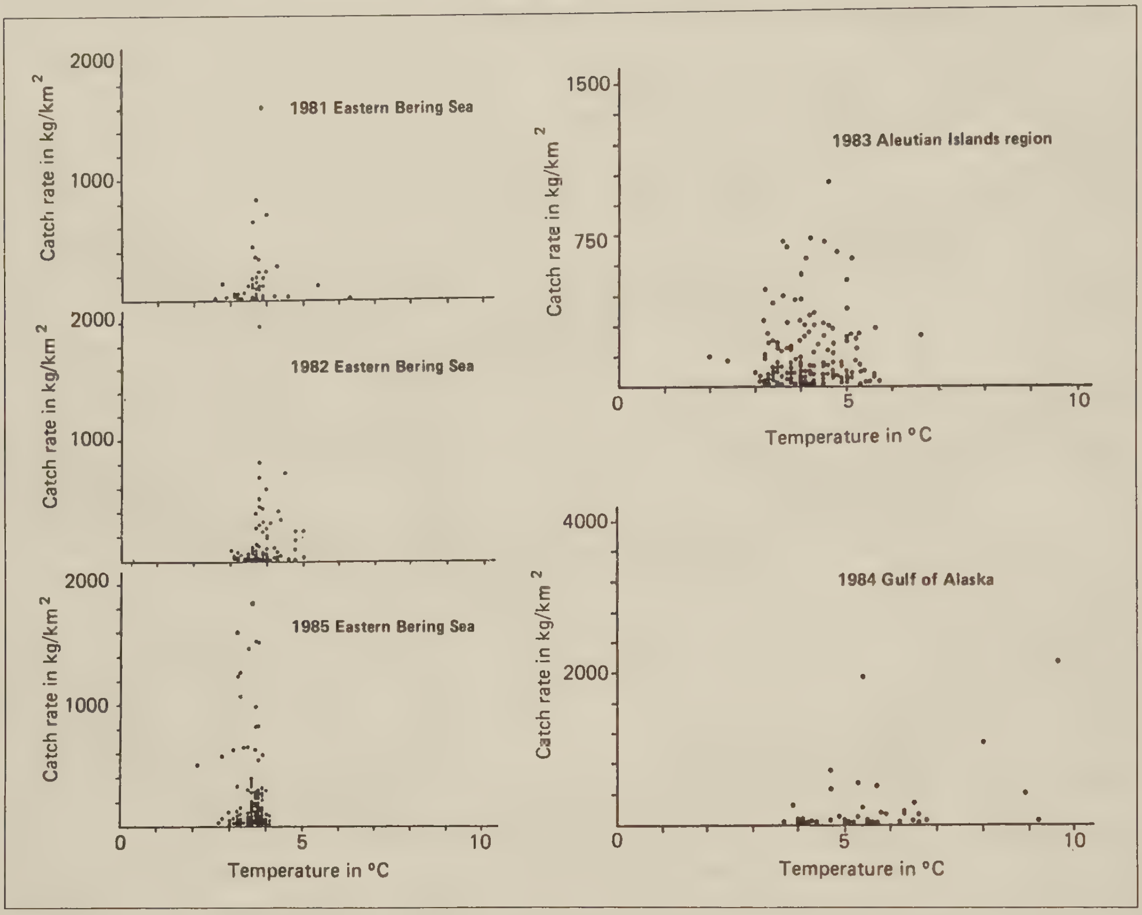

Figure 8.
Relationship of the catch rate to bottom water temperature in the eastern Bering Sea, Aleutian Islands region, and the Gulf of Alaska.

ship between skate distribution and water temperature. During the 1984 Gulf of Alaska survey, bottom water temperatures ranged from 4 to 10°C. Skates were encountered at stations where the temperature ranged from 4 to 7°C. Because the survey was conducted only from July to October (no wintertime sampling), the relationship between bottom water temperature and skate distribution remains unclear.

Data Limitations

An effective evaluation of trawl survey results and limitations of the data must also include a discussion of the factors which affect the accuracy and precision of bottom trawl surveys. These factors include skate movements between and within strata during the survey, which may result in multisampling or nonsampling of some concentrations (Wakabayashi and Bakkala 1985; West 1985), the accuracy of the vulnerability assumptions described earlier (catchability coefficient may be less than 1.0 or a herding effect may be present, i.e., >1.0), the ability of bottom trawls to sample skate abundance over rough bottom, and the assumption of a constant horizontal trawl opening throughout the survey for the "area swept" calculations. Caution must also be used when analyzing longline survey results to determine relative population increases or decreases because species which inhabit the same bathymetric niche as skates may also be competing for hooks and their change in abundance may mask real changes in skate abundance in the same area at the same time.

Summary

Skates comprise less than 3% of the total biomass of the eastern Bering Sea, Gulf of Alaska, and the Aleutian Islands as estimated from cooperative trawl surveys. By area, the skate complex accounted for 1.5% of the biomass of the eastern Bering Sea, nearly 1% in the Aleutian Islands, and 2.6% in the Gulf of Alaska.

Information from longline surveys conducted annually since 1979 indicates that relative skate abundance has increased since 1982 in the eastern Bering Sea, while decreasing slightly in the Gulf of Alaska between 1981 and 1986. Aleutian Islands skate abundance is less discernable from the surveys but exhibits a stable trend in 1985 and 1986.

In all areas surveyed skates were primarily distributed at depths associated with the continental slope or the shelf/slope break (greater than 200 m).

Biomass density per unit area estimates suggests that the productivity of skates in the Aleutian Islands is less than in the eastern Bering Sea or the Gulf of Alaska.

Skates were captured at bottom temperatures between 3 and 7°C from the three sea areas but the restrictive isotherms encountered during the summertime sampling resulted in inconclusive data for discerning the relationship between skate distribution and bottom water temperature.

Acknowledgments

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Deep-Sea Elasmobranchs Observed from Submersibles off Bermuda, Grand Cayman, and Freeport, Bahamas

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ABSTRACT

Deep-water sharks were lured to fish baits placed in front of stationary, quiet, and darkened submersibles (subs) used as blinds. Halogen, thallium iodide, and strobe lights were turned on for short scans, longer observations, and photography. Five subs were used from July 1986 to December 1987, which dived to depths of 584 to 1700 m off Bermuda, 244 to 978 m off Grand Cayman, and 564 and 624 m off Freeport, Bahamas. Fifty-four dives of 2.4 to 11.6 h duration were made and the sub settled on a ledge of the steep continental slope or on a plain. The largest and most common shark attracted was *Hexanchus griseus*, 200 to 550 cm TL ($N = 65$). Other sharks seen included *H. vitulus*, *Centrophorus granulosus*, *C. uyato*, *Dalatias licha*, *Isurus paucus*, *Galeocerdo cuvieri*, *Mustelus* sp., and species of *Etmopterus* and *Apristurus*. A pineal "window" was observed on the heads of many individuals of *Hexanchus griseus*, *Centrophorus granulosus*, *C. uyato*, and *Etmopterus* sp. A skate, probably *Raja teevani*, was photographed, and *Benthobatus marcida* and *Breviraja colesi* were collected.

Introduction

The sixgill shark, *Hexanchus griseus*, is the most common shark caught at 600 to 900 m by deep-sea fishermen off Bermuda, even though it has not been reported in the literature from this area. In the summer of 1985, we had the opportunity to photograph (with robot cameras) and to study specimens, caught by hook and line, of this species and other deep-sea fishes. Using the technique of deploying a baited automatic camera (Issacs and Schwartzlose 1975), one of us (EK) was able to photograph a few of these little known sharks, but most photos were unsatisfactory. In 1986 and 1987, we had the opportunity to use the submersible *Pisces VI* in Bermuda to make direct observations of fishes, especially sharks, at depths from 584 to 1700 m using the sub as a darkened, baited blind (Clark et al. 1986; Kristof and Chandler 1987). We could control the timing and direction of the camera for still and video photography. The Bermuda "Beebe Project" (named for the deep-sea explorer, William Beebe) led to sub dives off Grand Cayman with the *Pisces II*, *PC 1203*, and *PC 1802* submersibles (Clark 1988) and off Freeport, Bahamas in the *Johnson-Sea-Link II*. This paper summarizes only the elasmobranchs seen during 54 dives to depths between 244 and 1700 m at these locations. Teleosts representing over 20 families, giant isopods, and other invertebrates also seen will be reported elsewhere. This is part of an ongoing project to observe, study, and photograph deep-sea fishes.

Material and Methods

Submersible Dives

Although we made more submersible (sub) dives in Bermuda and Grand Cayman, we report here only those 54 dives (Table 1) in which we used bait and settled the sub for observations on the bottom. Occasionally, up to a third of the bottom time was spent seeking an appropriate place to park the sub or to relocate it. During this period of moving near the bottom we saw benthic bony fish and

Table 1.

Summary of 54 submersible dives to observe fishes, especially sharks, off Bermuda, Grand Cayman, and Freeport, Bahamas.

Location year	Submersible used	No. of dives	Dates of dives month/days	Depth m		Duration of dives			Time on bottom		
				Range	$\bar{x}$	Range	$\bar{x}$	Total	Range	$\bar{x}$	Total
Bermuda 1986	*Pisces VI*	3	7/6, 23 8/2	584–642	623	4h55′–11h38′	7h39′	22h57′	3h10′–9h51′	5h55′	17h46′
Bermuda 1987	*Pisces VI*	14	7/13, 21, 23, 24,[a] 25–27, 29, 31 8/10, 19–21	603–1700	972	2h23′–4h01′	5h36′	78h29′	1h24′–6h30′	3h37′	50h42′
Grand Cayman 1986	*PC 1802*	3	11/27, 29, 30	253–305	288	4h09’–4h38′	4h25′	13h15′	3h00′–3h24′	3h15′	9h46′
	PC 1203	1	11/28	244	244	2h21′	2h21′	2h21′	0h55′	0h55′	0h55′
Grand Cayman 1987	*PC 1802*	15	1/24, 25 2/24–27 3/26–29 5/26 6/27–30	297–311	304	3h44′–4h58′	4h21′	65h17′	2h46′–3h53′	3h09′	47h12′
	Pisces II	16	4/23, 24, 26, 27 5/24, 25, 27 11/26–29 12/18–22	373–978	834	4h26′–6h18′	5h22′	85h46′	2h14′–4h04′	3h05′	49h27′
Freeport, Bahamas 1987	*Johnson Sea Link II*	2	11/7, 8	564, 624	594	3h23′–4h01′	3h42′	7h24′	2h35′–3h15′	2h55′	5h50′
Total	5 subs used	54	from 7/6/86 to 12/22/87	244–1700	661	2h21′–11h38′	5h06′	275h29′	0h55′–9h51′	3h22′	181h38′

[a] Two dives in one day.

invertebrates and a few sluggish elasmobranchs lying on the substrate. In most cases, we avoided moving the sub once we found a good position. In one of the two dives made in the Bahamas the sub moved slowly along the bottom collecting specimens most of the time. In all other dives, once the sub was in place, we waited quietly in darkness. We turned off all lights except dim green lights similar in wave length and intensity to bioluminescence.

The bottom topography was usually fine sand over limestone with limestone outcroppings that were occasionally over 10 m high. These were called "haystacks" by the sub pilots. Photographs and paintings of some of these areas are delineated in Clark et al. (1986) and Clark (1988).

In Bermuda, using the *Pisces VI*, we went to depths of 584 to 1700 m. In the summer of 1986, three dives were made near lat. 32°22′N, long. 65°00′W; in the summer of 1987, 14 dives were made near 32°17.0′N, 64°40.5′W; 32°22.11′N, 64°56.7′W; 32°23.0′N, 64°57.4′W; and 32°24.1′N, 65°00′W. In November 1986 and from January to December 1987 we made 35 sub dives off the west coast of Grand Cayman. Using the *PC 1203* and *PC 1802* our shallowest dives were 297 to 311 m at 19°19′N, 81°21′W. For deeper dives (373 to 978 m) we used the *Pisces II* at lat. 19°19′N from the shallow "haystacks" (high rock formations) at 81°21′W to our deepest dives at 81°24′W. We made six dives to 930, 944, 953 (twice), 960, and 978 m in the trough between Grand Cayman Island and Cayman Bank (22 m depth), that were deeper than depths indicated on charts (500 fathoms or 914 m).

The nineteen shallow dives (244 to 311 m) made off Cayman were "night dives," i.e., we left the surface in late afternoon, dusk, or after dark so that most of our bottom time would be without any trace of sunlight. These dives were planned to take place within seven days before or after the new moon for maximum darkness. Sixteen deeper dives were made at any convenient time of day, usually during daylight. In all but one dive (at 373 m) we experienced aphotic conditions (no sign of sunlight detected by our dark adapted eyes) between 579 and 978 m, excepting the submersible's artificial lights and ambient bioluminescence. The two dives in the Bahamas were made on 7 and 8 November 1987, 3.5 mi South of Freeport, Grand Bahama lat. 26°27.53′N, long. 78°48.12′W and 26°28.86′N, 78°49.57′W to 623 m and 550 m respectively.

The water temperature could be recorded for only some dives. The *Johnson Sea Link II* has a built-in thermometer. Temperatures during our November 7 and 8 dives varied from the surface (18.0°C) to the deepest dive at 624 m (9.6°C). In Cayman we attached temporary thermometers

Table 2.

Elasmobranchs observed from submersibles during 54 dives to depths of 244 to 1700 m in 3 areas of the northwest Atlantic, July 1986–December 1987. GC = Grand Cayman; BE = Bermuda; FB = Freeport, Bahamas; SD = Sub Dives.

			No. of individuals[a]			
Species	Estimated TL or DW[b] (cm)	Depths observed (m)	35 SD GC	17 SD BE	2 SD FB	54 SD total
1 *Hexanchus griseus* (sixgill shark)	200–550	299–1560	23/25	42/56	—	65/81
2 *Hexanchus vitulus* (bigeye sixgill)	75–150	302–311	8	—	1	9
3 *Centrophorus* sp. (gulper shark)	45–180	579–978	36/43	20/33	4	60/80
4 *Dalatias licha* (kitfin shark)	90–120	944–1640	1	2	—	3
5 *Mustelus* sp. (smoothhound)	45–120	300–808	9/12	4	1	14/17
6 *Galeocerdo cuvieri* (tiger shark)	250	305	1	—	—	1
7 *Isurus paucus* (longfin mako)	280	760	1	—	—	1
8 *Apristurus* sp. (cat shark)	30–45	876–944	4	—	—	4
9 *Etmopterus pusillus* (lantern shark)	20	564–922	—	1	2	3
10 Miscellaneous sharks	20–150	300–800	4/6	6	1	11/13
11 *Raja teevani*	85 DW	881	1	—	—	1
12 *Breviraja colesi*	14	623	—	—	1	1
13 *Benthobatus marcida*	7–8	564	—	—	3	3
14 *Narcine* sp.	20	305	1	—	—	1
Total			89/103	75/102	13	177/218

[a] Minimum/maximum.
[b] DW = disc width.

to the submersible on a few shallow dives, which recorded 24°C at the surface and the surprisingly high temperature of 18.4°C at 305 m. Our thermometers broke on deeper dives. We were not able to record water temperature on the *Pisces II* and *IV* dives, which went to deeper and colder waters where the inside sub wall became cold and wet to the touch.

Method of Counting and Measuring Elasmobranchs

Counts of skates and rays seen on each dive were precise because we saw few individuals and could keep track of each one. The sharks, however, especially the numerous individuals of *Hexanchus griseus* and *Centrophorus granulosus*, were sometimes difficult to tell apart. Individuals that repeatedly came back could often be identified by their markings and colors or unique spots. Sometimes, owing to the angle of approach, distance away, or lack of distinctive markings, we could not tell if a shark was a new individual or one that had returned to the bait. Therefore, in Table 2, we give the lowest and highest counts for each dive and have totaled these for the count of each species. There was no evidence from our several thousand photographs and many hours of video that the same shark ever came back to our bait on separate dives even when we went back to the same site on consecutive days and expected occasionally to see a shark we had seen on a previous dive. There is a possibility, therefore, not accounted for in our method of totalling the individual sharks, that we may have counted a nondescript individual shark twice when it appeared in another dive. The sum counts given for sharks in Table 2, even the conservative minimum (sum of the number of individuals we are sure we saw on each dive), may reflect one or a few individuals counted twice.

Measurements of specimens observed are given in total lengths (TL) for sharks and disc widths (DW) for skates and electric rays. Except for the few specimens collected, all measurements are estimations based, whenever possible, on the known length of some object (bait bag, cage, projections from the sub) close to the shark. Visibility was good once the sediment stirred by the sub settled (1 to 5 minutes) and we could see between 20 and 50 meters when lights high on the sub were turned on.

Bait

The bait we used in Bermuda was usually tuna and squid. In Grand Cayman we used a combination of squid, fish, sea turtle offal and blood, and cow offal. We seemed to get the best results attracting sharks when we used tuna (Table 3). Because tuna is scarce in Bermuda and Cayman, we brought frozen tuna parts from the mainland for bait on all the 1987 dives in Bermuda and most of the later dives in Cayman. The bait was placed (usually frozen) in burlap bags, wire cages, or plastic mesh onion bags. Blood or blood and ground offal were placed in plastic quart containers that we punctured just before the dive. This bait was usually deployed when we reached a good area on the bottom and the sub then backed away from it to a distance

Table 3.
A comparison of the number (minimum/maximum) of sharks per hour of bottom time (hBT) attracted to submersibles with and without the use of tuna bait.

		Sharks attracted[a] and bottom time						Sharks attracted per hBT	
		Totals		Without tuna		With tuna		Without tuna	With tuna
Areas	No. of dives	Sharks	hBT	Sharks	hBT	Sharks	hBT	Sharks/hBT	Sharks/hBT
Cayman	35	83/97[a]	106.8	20/23[a]	54.0	63/74	52.9	0.45/0.50	1.19/1.40
Bermuda	17	75/102	60.5	1	5.5	74/101	55.0	0.18	1.35/1.84
Bahamas	2	9	5.8	9	5.8	—	—	1.64	—
All 3 areas	54	167/208	173.1	30/33	65.3	137/175	107.9	0.53/0.57	1.27/1.63

[a] We did not count the 4 *Apristurus* sp. we found lying on the bottom that did not come over to the bait.

of 2 to 8 m. In some cases the bait was tied loose or left in containers on the front of the sub. There is a strong possibility that Cyalume[1] sticks that we used also attracted sharks to the bait. In the Bahama dives octopus, squid, cow's liver, and blood and raw hamburger meat were used as bait.

Lights and Cameras

All the subs carried several bright halogen lights mounted outside and inside the sub. In addition a dim-green thallium-iodide light was mounted on the outside of *Pisces VI*. We usually tied from two to six Cyalume chemical stick lights in the bait bag or wire mesh cage. The Cyalume sticks and thallium iodide lights did not seem to bother any of the animals but the halogen and strobe lights caused most of the fish, except blind species, to become shy or dart away. Therefore we kept the halogen lights turned off most of the time except when photographing.

Several types of cameras were used. Various 35 mm hand-held still cameras and compact video cameras were used from inside the sub. An offload camera was used with the *Pisces VI* during summer 1986. This remote camera, a Benthos model 374 made in North Falmouth, MA, had a 15 mm lens and took 400 exposures on each roll (Vericolor Kodak, 160 ASA). It was controlled by a photo-activated switch and had two strobe lights (350 watt/s). The system was built by Al Chandler at National Geographic. A Benthos camera model 378 was mounted on the *Pisces VI* in 1987 along with two Sony CCD color cameras (4.8 mm lenses) for 3D television. A prototype RCA CCD video camera with a one million ASA black and white video tape was also used on most of the dives in Bermuda in 1987.

Results

The number of elasmobranchs seen in the areas of Grand Cayman, Bermuda and the Bahamas is summarized in Table 2. During the 54 dives in these areas (Table 1), we saw a total of at least 177 individuals of at least 14 species.

Sharks Attracted to Tuna Bait

Sharks seemed to be more attracted to bait that consisted entirely of tuna or had tuna mixed in with squid and other bony fish. Table 3 shows the total number of sharks actively attracted to the bait (167 minimum/208 maximum) during 173.1 hours of bottom time and shows that the number of sharks attracted by tuna or tuna mix per hour of bottom time (1.27/1.63) was more than twice the number (0.53/0.57) attracted without tuna.

Species Accounts

***Hexanchus griseus* (Bonaterre, 1788), Sixgill Shark—** This was the largest and most common species of elasmobranch we observed from the subs and had the widest depth range (Table 2, Figs. 1,2,3). Some individuals seemed hardly disturbed by our bright lights while others swam or jerked away suddenly, sometimes bumping into the sub when the lights were turned on. In one violent reaction of this type, the distal ends of the claspers of a large male expanded and emerged from the clasper sac. Undisturbed individuals moved around so slowly that replays of the video tape look as if they had been filmed in slow motion. They were usually timid in getting started but once an individual bit into the bait it usually returned. It was not unusual for one to return over and over for an hour or more and even to follow the sub for a short time when we finished and started to lift off the bottom.

The 65/81 individuals we saw had great variation in color and markings, ranging from gray or tan, with pale counter-

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[1] Small, translucent, plastic tubes filled with chemicals, that when activated produce a dim light. American Cyanamid Co., Milton, FL 32570.

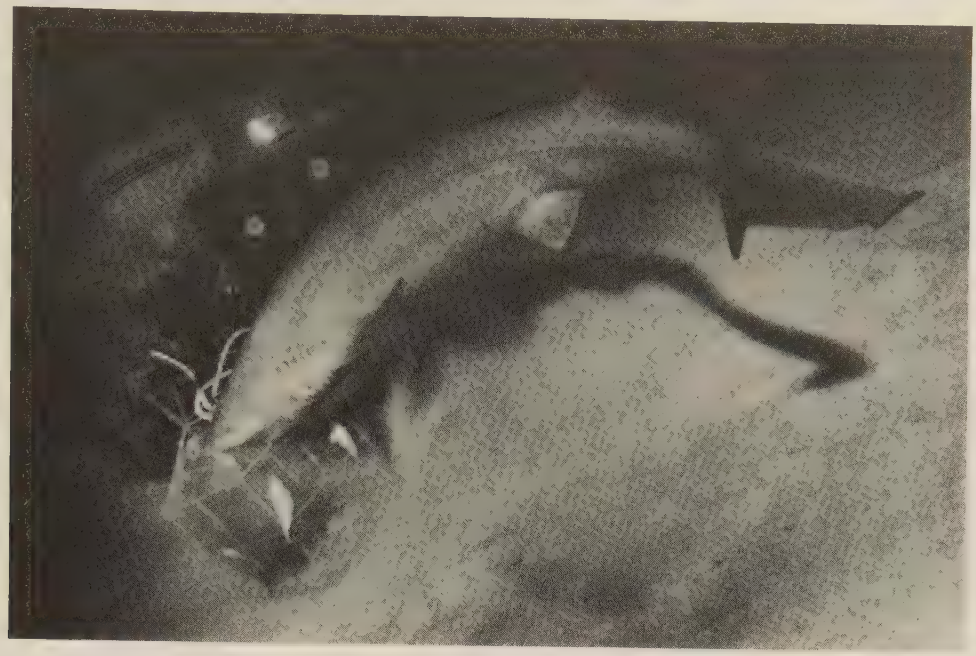

Figure 1.
Hexanchus griseus, immature female about 280 cm TL, attracted to the cage (baited with fish) deployed from manipulator arm of *Pisces VI* submersible in background; depth 600 m, Bermuda. Photo taken by an offload camera.

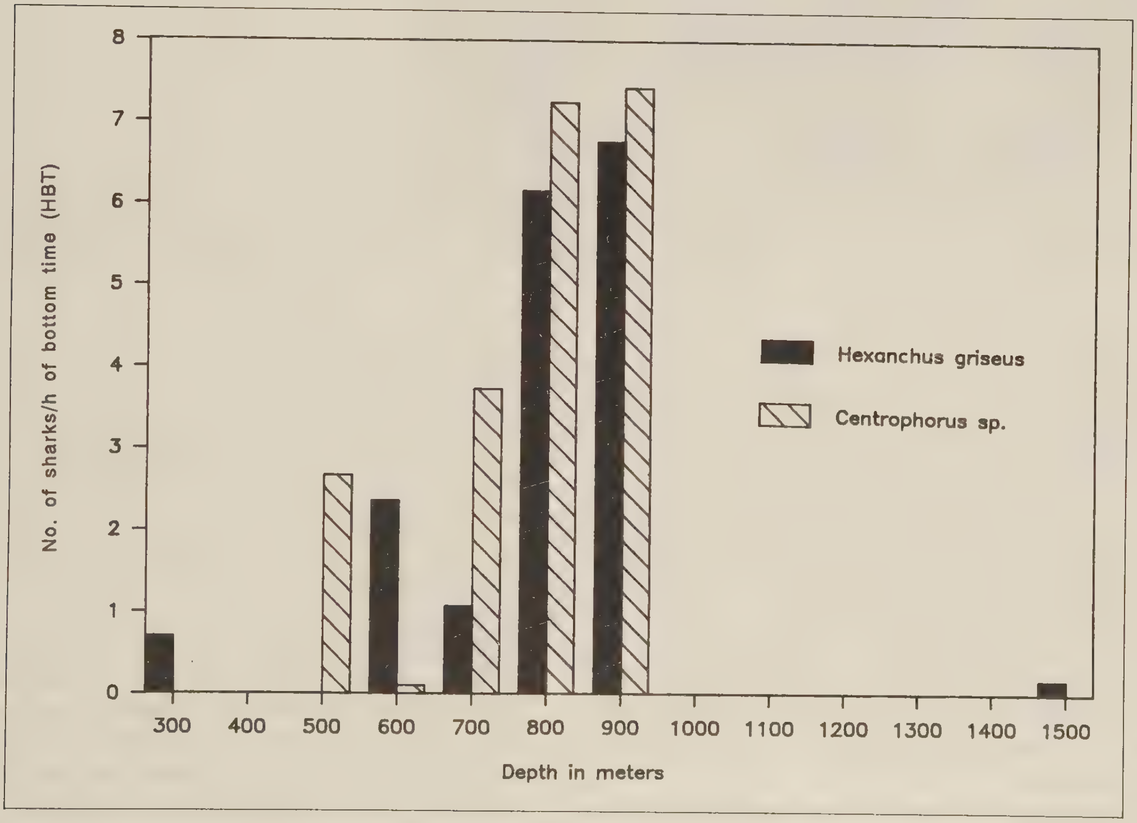

Figure 2.
Numbers of sharks (*Hexanchus griseus* and *Centrophorus* species) seen from subs per hour of bottom time at different depths in Bermuda and Grand Cayman (1986 and 1987).

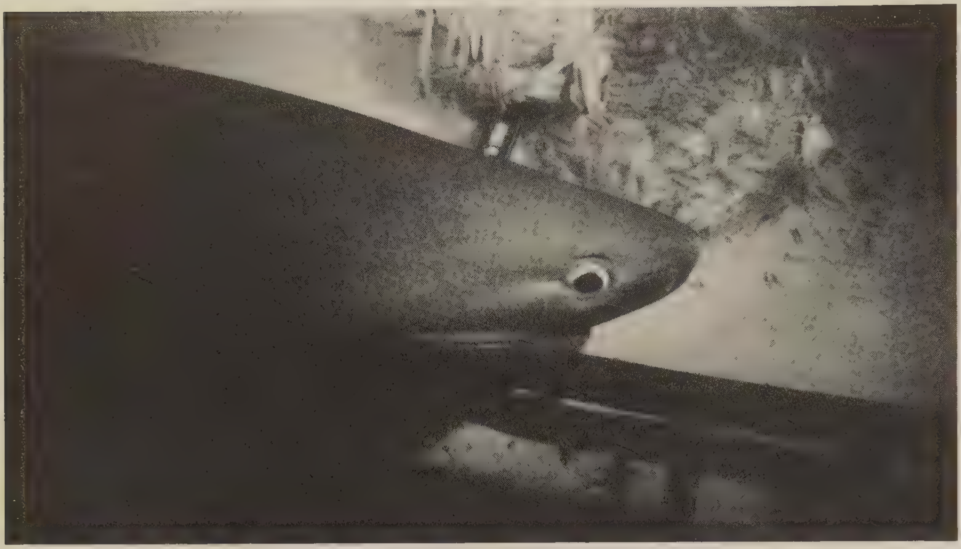

Figure 3.
Hexanchus griseus, mature male about 350 cm TL at depth 305 m, Grand Cayman. Photo taken from inside the acrylic ''bubble'' window of the *PC 1802* submersible. In the background the bait cage and burlap bag (with bait and squid) has attracted hundreds of shrimps and a crab.

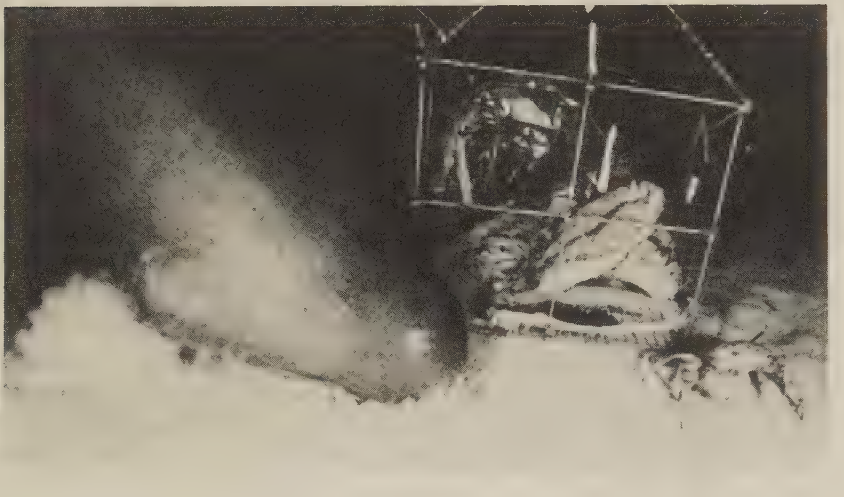

Figure 4.
Hexanchus griseus adult male, mouthing the sand in front of the bait cage, depth 600 m, Bermuda. Top of head shows the pineal ''window''.

shading ventrally, to a dark chocolate-brown without countershading (i.e., as dark ventrally as dorsally). Many were weakly to heavily spotted with uneven brown spots of two cm or less in diameter. We found no correlation between the coloring and the size, sex, or depth of the sharks. About 25% of these *H. griseus* sighted and photographed with still and video cameras had a conspicuous white spot on the top of the head exactly midway between the eyes (Fig. 4). This unpigmented area is probably the same ''pineal window'' we have examined in other sharks (see *Centrophorus* and *Etmopterus*). We did not notice a pineal spot on the seven specimens of *H. griseus* we caught in Bermuda (see below).

The largest *H. griseus* that could be identified as a male was about 430 cm TL. The claspers of males 260 cm and larger appeared to be fully developed judging from the length and fullness of the pelvic fin sac in which the claspers were located. The largest female was observed in Bermuda at a depth of 922 m. It was huge in abdominal girth and was the only one that appeared to be pregnant. It was estimated at 550 cm TL. The height of the tail was estimated fairly accurately at slightly over 100 cm when it passed next to the bait cage. The other females ranged from 210 to 460 cm TL and were all slim bellied like the specimen in Figure 1.

We examined five females and two males freshly caught on hooks baited with squid set near the bottom in about 760 m depth off the west end of Bermuda during May 1985, June and July 1986, and June 1987. The females were all virgins: the smaller ones (220, 298, 314, and 350 cm TL) were pale gray with almost white undersides, the largest (358 cm TL) was as dark brown ventrally as it was dorsally.

The 350 and 358 cm females appeared near ready to mate (Clark and von Schmidt 1965). The hymens covering the double openings to the paired vaginas of each female were very thin and could be easily torn open. Without forcing, both females had a larger opening through the left hymen (which would just admit a 2.0-cm diameter probe) than on the right hymen which had an opening of about 0.5 cm. The three smaller females had small (<0.5 cm) openings in a tough hymen on both sides. The ovaries of the two largest females had hundreds of small white eggs (<0.2 cm diameter) and larger yellow eggs (0.7 to 1.7 cm diameter). There were 65 yellow eggs in the right and 47 in the left ovary of the 350 cm female. There were 53 in the right and 50 in the left ovary of the 358 cm female. The two males, 282 and 287 cm TL were dark gray with pale gray countershading. The claspers, inside the pelvic fin sacs, appeared mature on the larger shark (the clasper head opened easily) and immature on the smaller. The size of maturity in males is not known (Castro 1983) but Ebert (1986b) reported a mature male at 325 cm TL. The smallest female with embryos was reported by Ebert (1986a) as 421 cm TL. Litters of young are large (Ebert 1986b), up to 108 pups (Castro 1983).

The stomach contents of the *H. griseus* specimens we examined included the partly digested and rotting remains of the hind part of a cetacean, a shallow water moray eel, *Gymnothorax moringa*, and the body of a large (150+ cm TL) oilfish, *Ruvettus pretiosus*, the head of which was found on another hook in the same series of gear that caught the *H. griseus*.

Although usually considered a deep-water species, *H. griseus* has been photographed and videotaped by scuba divers as shallow as 18 m in cool surface waters of British Columbia (Rick Brock, 8302 45th Pl. W., Mukilteo, WA 98275, pers. commun., Fall 1984; Bob Zielinski, Hornby Island Diving, Hornby Island, B.C., V0R1Z0, Dec. 1989). During the Beebe Project, telemetry trackings were made of two females (estimated TL 3.4 and 4.0 m) caught in about 550 m depth. During 68.5 hours of tracking, the smaller female stayed between 600 and 1240 m excepting one 15 minute excursion to 1500 m, 10 hours after she was tagged. The larger shark, during 27 hours of tracking, stayed between 600 and 1100 m (Frank Carey, Senior Scientist, Woods Hole Oceanographic Institution, MA 02543, pers. commun., Sept. 1987). This data fits our findings (Fig. 2) for we found *Hexanchus griseus* quite common when we made dives to depths between 550 and 1000 m, rare on our dive to 1500 m, and absent on the dive to 1700 m. Two dives we recently (October 1988) made in the *Alvin* in Monterey Canyon to 2819 and 3586 m also produced no sharks. *H. griseus* is common off California but our 40 pounds of tuna bait on each dive attracted only quantities of teleost fishes. From this evidence it appears that *H. griseus* rarely goes to depths of 1500 m and deeper.

Along with the sevengill shark, *Notorynchus cepedianus*, the sixgill shark *H. griseus* is sold as food under the name cowshark in California where it has been reported as the most commonly marketed elasmobranch (Frey 1971). As with many other deep-sea sharks used as food (e.g., *Dalatias licha*, several species of *Centrophorus*), *H. griseus* does not have the objectionable "sharky" smell of shallow-water sharks which must be bled, soaked in brine, lemon juice, or vinegar to remove excess urea (Cook 1985). The Japanese serve deep-sea sharks raw (sashimi) without this preparation. However, the urea content of deep-sea sharks has not been tested and we do not know if it is lower than shallow water sharks. Perhaps deep-sea sharks lack the microbes (*Vibrio* sp?) that are found in shallow water sharks and that are responsible for breaking down urea which causes the unpleasant smell once the shark has died (D. Jay Grimes, Univ. of New Hampshire, Durham 03824, pers. commun., Dec. 1987).

***Hexanchus vitulus* Springer and Waller, 1969, Bigeye Sixgill Shark**—One mature male, 150 cm, approached the bait in the Bahamas on 7 November 1987, 30 min. after we reached a sandy, wide plain at 621 m. Water temperature was 9.6°C. Eight specimens, 75 to 150 cm, were attracted to the bait off the Caymans at 302 to 311 m on 7 separate dives on 24, 25 January, 24 February, 26 March, and 27, 28, 29 June 1988. The two largest specimens were mature males, their clasper covers reaching almost to the anal fin. Their eyes were noticeably larger and seemed black compared with *H. griseus*. In all individuals the head and body was pale to medium gray or tan, lighter on the underside (countershaded) without any of the dark spots commonly seen on *H. griseus*. In individuals 75 to 120 cm TL, the fins were shaded darker (brown to blackish brown) on their distal half and had a white tip or margin. The white margins of these fins were most conspicuous on smaller individuals (Fig. 5). A pineal window was not conspicuous on any individuals.

Bigeye sixgills did not stay near the sub for more than a few minutes, especially if the bright lights were turned on. Individuals stayed in the vicinity and returned to the sub repeatedly when its lights were turned off. They never tried to eat the bait but often swam within 0.5 m of the bait and bait cage.

Cayman fishermen have caught this shark when fishing for snapper at depths of about 300 m. One of us (EC) was able to examine the jaws and dried skin of a female of about 150 cm TL caught 7 April 1987 (Fig. 6). Less than 50 *H. vitulus* are currently caught yearly by the large Mexican shark fisheries and then only when they fish near deep water at the edge of Campeche Bank off northern Yucatan (Ramon Bonfil, fisheries biologist, National Fisheries Institute of Mexico 97320, pers. commun., Dec. 1987).

***Centrophorus* Species, Gulper Sharks**—Gulper sharks were observed at depths from 579 to 978 m and were the most common elasmobranchs attracted to our subs ($N = 60/80$) at these depths (Table 2, Figs. 7,8,9). Although they

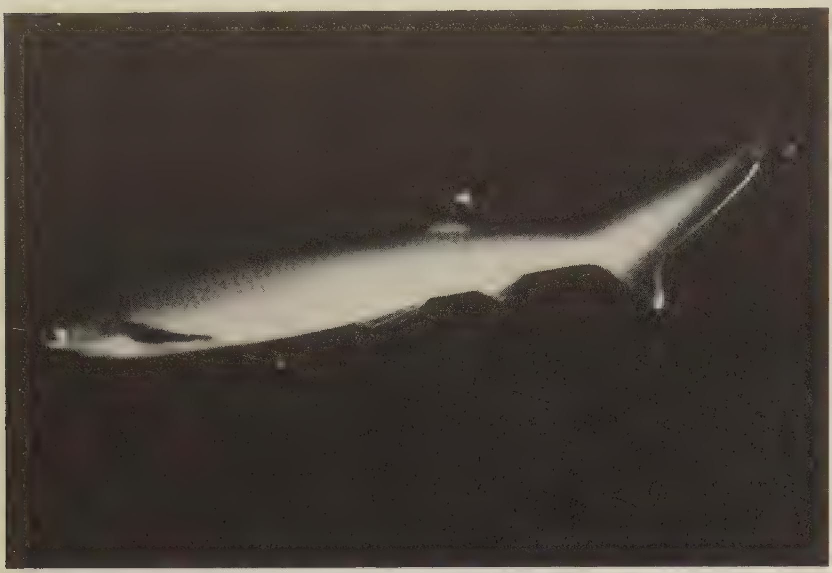

Figure 5.
Hexanchus vitulus about 100 cm TL at depth of 305 m, Grand Cayman, showing fins with dusky margins, edged in white. (Photo by Marjorie L. Bank.)

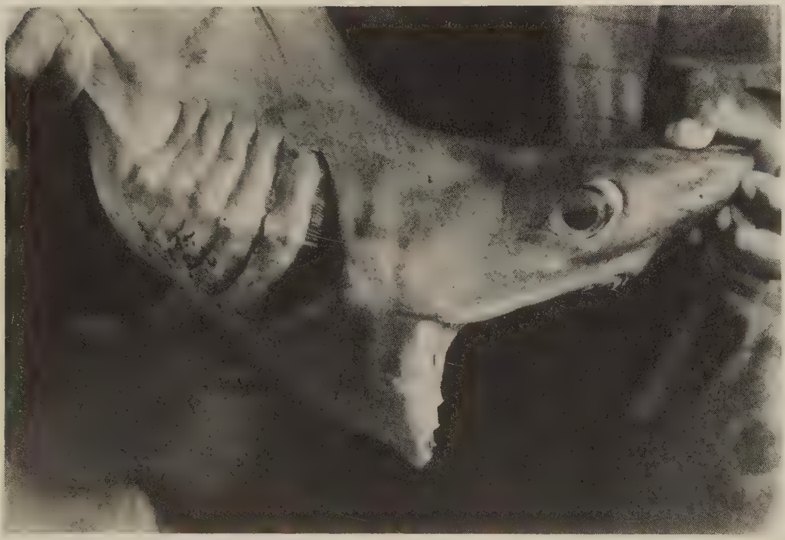

Figure 6.
Hexanchus vitulus, head of female, about 150 cm TL, caught at 300 m, 7 April 1987, Grand Cayman. (Photo by Carol Winker.)

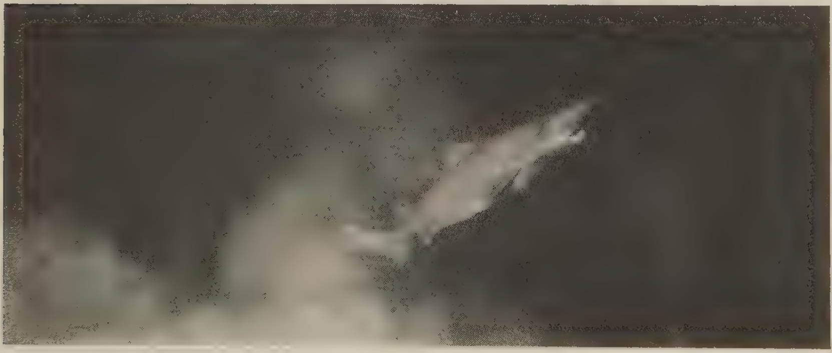

Figure 7.
Centrophorus species, probably *C. granulosus*. This appears to be an adult female, possibly pregnant, about 130 cm TL. Depth 580 m, Grand Cayman.

did not rival the numbers of *Hexanchus griseus*, it was common to see four or five and as many as 10 swimming around the bait at one time. On only two dives did we see more than two *Hexanchus griseus* at one time. *Centrophorus* did not seem disturbed by the bright lights, each other, and an occasional large *H. griseus* that came in and fed alongside them. *Centrophorus* consumed the bait readily and was the only shark which we observed that ate until their abdomens were visibly distended. Even then some kept feeding and spitting out the food.

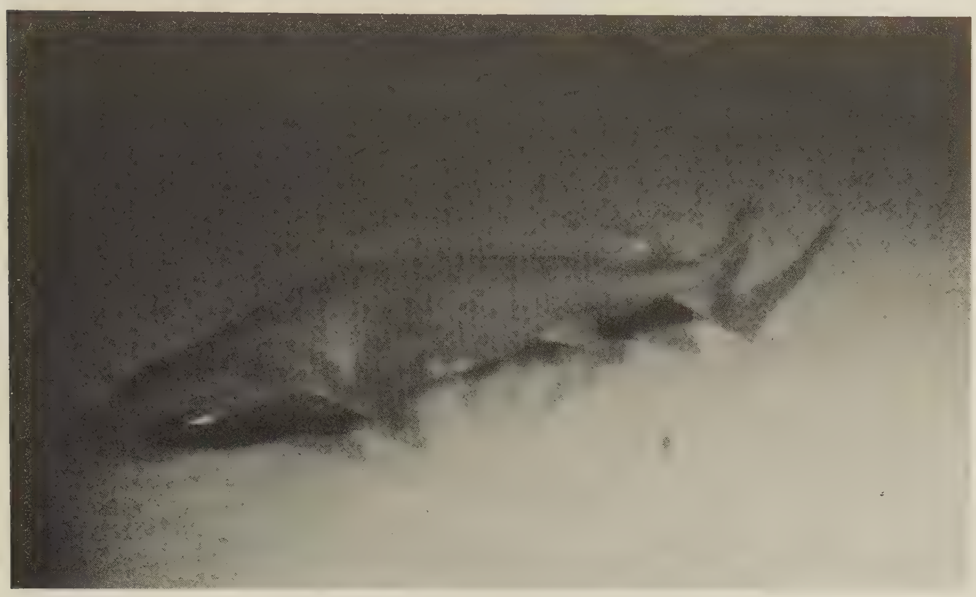

Figure 8.
Centrophorus granulosus, about 120 cm TL, showing a white spot on left side of second dorsal fin which was used as a natural marker for this individual. Depth 914 m, Grand Cayman.

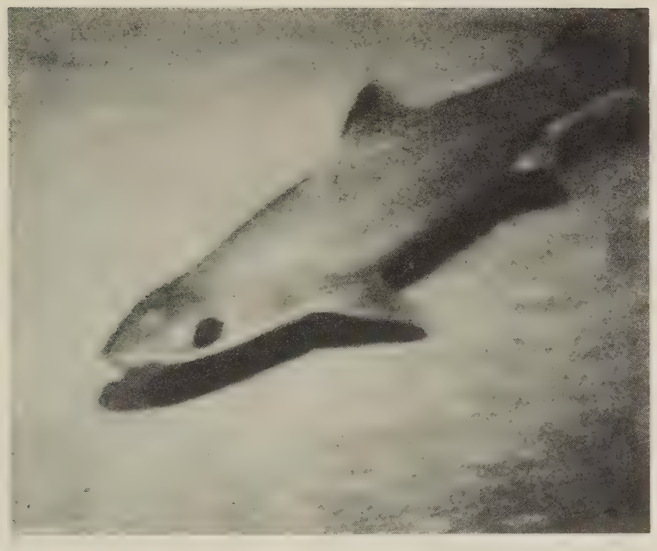

Figure 9.
Centrophorus uyato about 80 cm TL, showing the pineal "window." Depth 790 m, Grand Cayman.

About half of the adult gulper sharks appeared to be *Centrophorus granulosus* (Bloch and Schneider, 1801). At least 30% of the adults (130–150 cm TL) could be identified as *C. uyato* (Rafinesque, 1810) based on their flatter head, larger eyes, and the color pattern of the fins. In *C. uyato* the upper third of the two dorsal fins had conspicuous triangular black tips and the terminal third of the upper lobe of the caudal fin was dark or white with a dark tip. The pectoral, pelvic, and lower lobe of the caudal fine was dusky and had a pale margin. In *C. granulosus* the color of adults was a more uniform tan with countershading or darker, gray or brown, without countershading (Fig. 7). Many individuals could be told apart by one or two white spots, as large as 4.0 cm diameter, irregularly placed on the left or right side of the body or fins, usually on the upper caudal lobe or dorsal fins (Fig. 8). In over 90% of the adults of *C. granulosus* and/or *C. uyato* the top of the head showed a light or white spot (lacking pigment) on the center of the head between the eyes (the pineal window) (Fig. 9). This spot was thought to be a luminescent organ by Gilat and Gelman (1984) from their underwater photographs of *C. granulosus*. Many young *Centrophorus* individuals (50 to 100 cm TL) had conspicuous white margins on all fins except the second dorsal, although some had a trace of white on the second dorsal fin also. In the smallest individuals, the broad white margin on the upper caudal lobe occupied half of the lobe and stood out like a white flag. These young sharks swam around the bait faster, fluttering their fins and turning more often than adults. We could not be sure of the species of these small sharks although some of them seemed to be *C. uyato* or *C. granulosus* because the white markings were less conspicuous in larger specimens approaching 100 cm TL. In one uniformly dark adult specimen of *Centrophorus*, a close-up photo revealed an absence of the prolonged rear tip of the pectoral fin which is characteristic of *C. granulosus*, but the presence of tiny dark "granules" scattered on the skin, typical of *C. granulosus*. On another adult we noted a ragged edge to the fins as shown in Compagno (1984, p. 36) for *C. acus*. We suspect at least three species of *Centrophorus* may be included in our sightings, photographs, and videotapes. The short claspers of adult males in this genus made it more difficult to determine the sex of even the largest specimens observed.

Centrophorus granulosus and *C. uyato* are fished in bottom trawls and by hook and line for their livers rich in valuable squalene oil. They are also eaten dried, salted and fresh and processed for fishmeal (Compagno 1984). Gilat and Gelman (1984) believe a commercial fishery for *Centrophorus* could be developed in the eastern Mediterranean on the sea floor at depths of 500 to 1000 m, where their studies and photographs showed *C. granulosus* to be the most abundant species of fish.

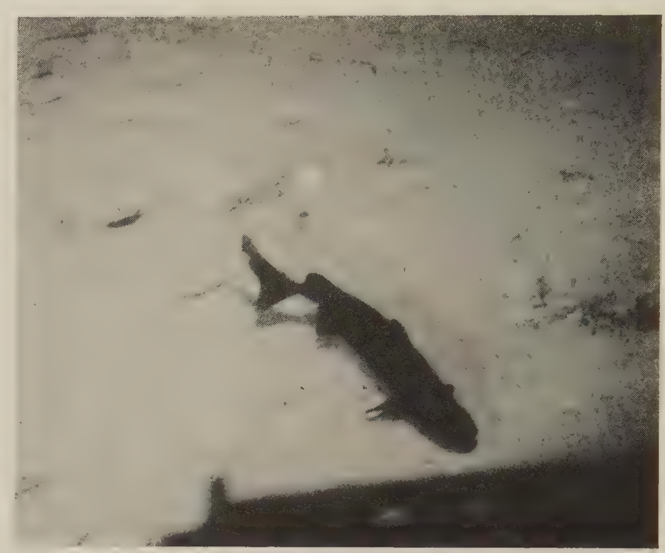

Figure 10.
Dalatias licha about 100 cm TL. Depth 944 m, Grand Cayman.

***Dalatias licha* (Bonnaterre) 1788, Kitefin Shark**—We observed and photographed two individuals in Bermuda, about 100 to 130 cm TL at 1,560 and 1,640 m depth and one about 100 cm TL in Cayman at 944 m (Fig. 10). The strong teeth and tongue and fleshy lips of *Dalatias* (Figs. 11, 12a, b) indicate that it may at times have a similar feeding behavior to *Isistius*, a smaller related genus of "cookie cutter" sharks which apparently bites much larger prey with its large interlocked lower-jaw teeth (Strasburg

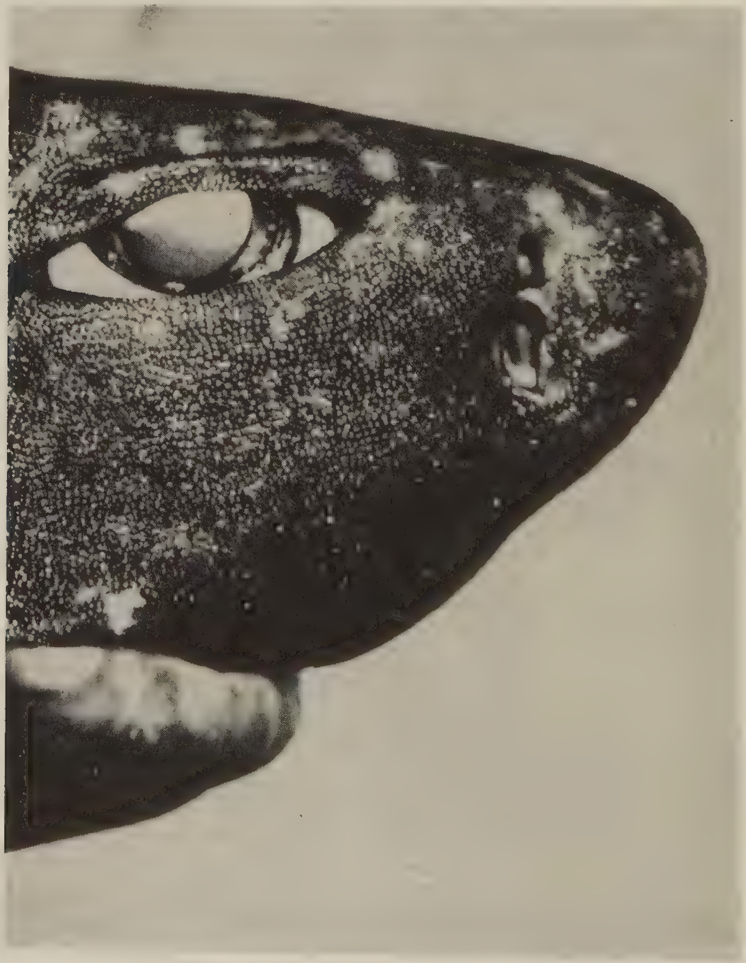

Figure 11.
Dalatias licha about 150 cm TL freshly caught by fishermen off the coast of Yaizu, Japan showing fleshy lower lip. (Photo by David Doubilet.)

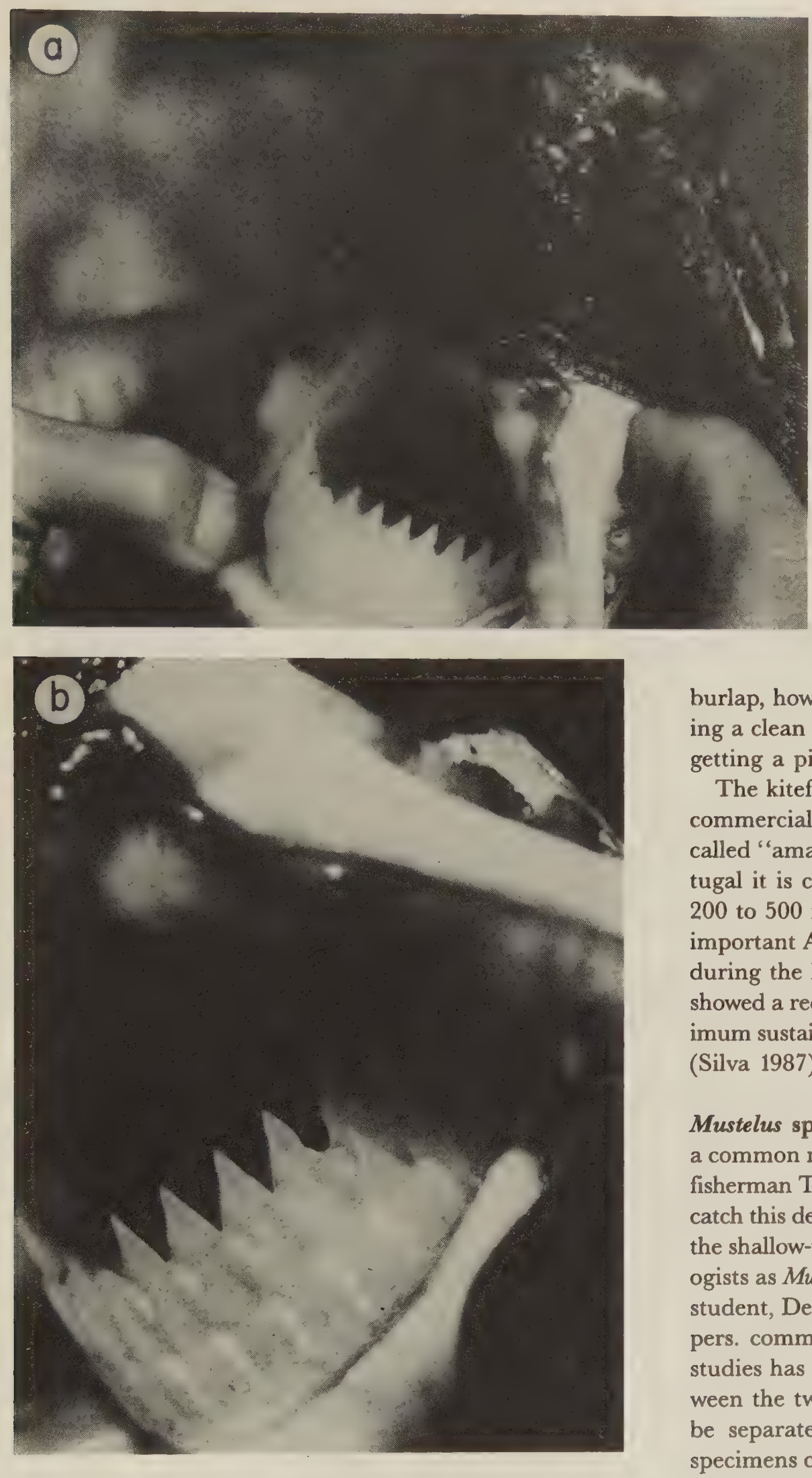

Figure 12.
Dalatias licha, same specimen as in Fig. 11. (a) shows strong interlocking teeth in the lower jaw. (b) Close up of teeth showing the front row about to be shed in one unit, like a denture. (Photos by David Doubilet.)

1963), spins around to cut a circular wound, and then uses lips and tongue to create a vacuum to pull out a plug of flesh (Johnson 1978; Heemstra 1980). Our videotape of *Dalatias* feeding on our bait in Bermuda showed some spinning action after the initial bite on burlap wrapped tuna bait, tied onto the manipulator arm (Fig. 13a, b). The loose burlap, however, appeared to hinder the shark from making a clean cut and the shark finally pulled away without getting a piece of the bait.

The kitefin is cosmopolitan in distribution. It is fished commercially with long lines off Yaizu, Japan, where it is called ''amazame'' (Clark 1981, 1987). In the Azores, Portugal it is caught with bottom nets and lines at night in 200 to 500 m (Silva 1983, 1987). It has become the most important Azores demersal fish species, in weight, caught during the last 7 years. In 1986 the catch per unit effort showed a reduction and indicates overexploitation. A maximum sustainable yield was calculated to be 933 tonnes/year (Silva 1987).

***Mustelus* sp., Smoothhound**—''Bigfin gummy shark'' is a common name given to this shark by Bermuda deep-sea fisherman Teddy Tucker. Fishermen in Bermuda frequently catch this deep-water shark and recognize it as distinct from the shallow-water ''gummy shark,'' well known to ichthyologists as *Mustelus canis* (Mitchell). Karen Moody (graduate student, Dept. of Zoology, University of Maryland 20742, pers. commun., Feb. 1988) in EM (electron microscopy) studies has found differences in the dermal denticles between the two types of Mustelus that may prove them to be separate species or subspecies. We examined three specimens caught in Bermuda and observed at least 14 individuals 45–120 cm TL during sub dives in Cayman, Bermuda and Bahama at depths from 300 to 808 m. They were pale, lack countershading, and had dark fins. The distal margins of the first dorsal, pelvic, and anal fins are usually edged with a barely noticeable white fringe. The distal margin of the caudal fin was conspicuously white (Fig. 14). The two dorsal and pectoral fins seem larger and the first

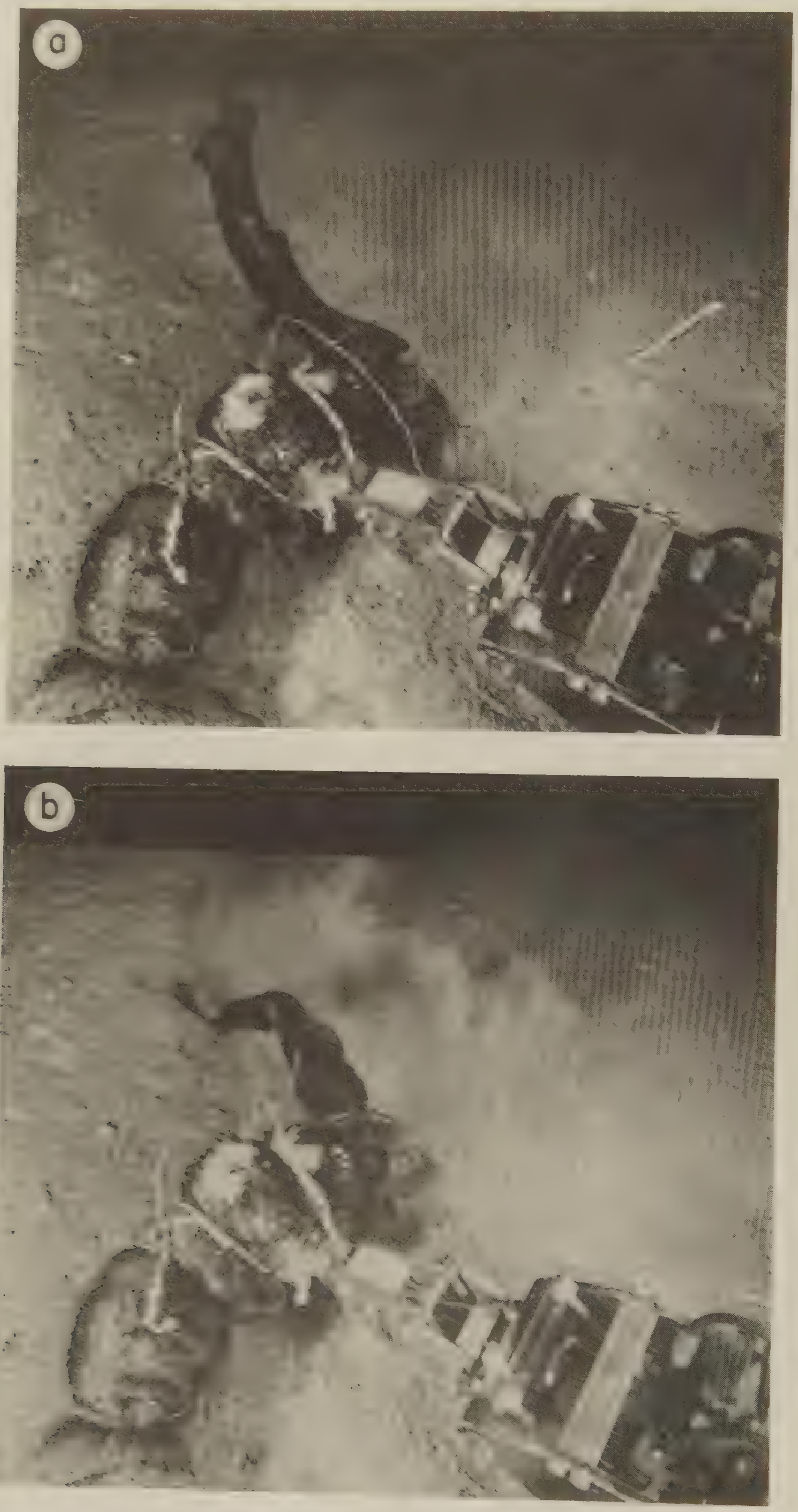

Figure 13.
(a) *Dalatias licha*, about 100 cm TL at 1640 m, Bermuda. Shark is biting on a burlap bag filled with tuna and attached to the manipulator arm of the *Pisces VI* submersible). (b) *Dalatias licha*, same specimen as above, vigorously turning its body in an aborted "spin" in an attempt to take a piece out of the bait bag.

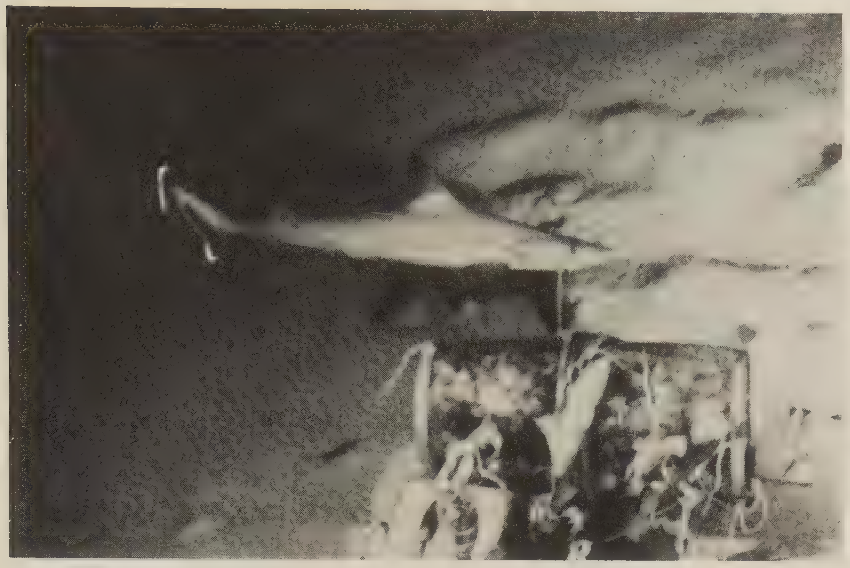

Figure 14.
The "deep-water gummy shark", *Mustelus* sp. about 70 cm TL. Depth 297 m, Grand Cayman. (Photo by José Castro.)

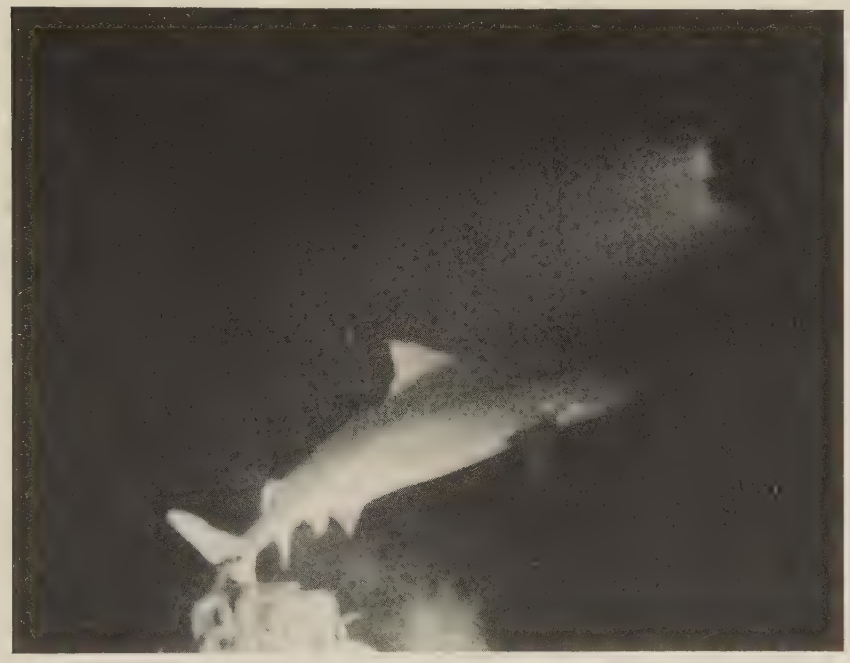

Figure 15.
Tiger shark, Galeocerdo cuvieri, female about 260 cm TL. Depth 305 m, Grand Cayman.

dorsal more pointed than the shallow-water *M. canis*. The bigfin gummy shark seemed shy and usually darted away when the bright lights were turned on. From our field observations, it lacked a pineal window.

Galeocerdo cuvieri **(Peron & LeSuer, 1822), Tiger Shark—** One young female, 250 cm TL, swam slowly and circled the bait cage (Fig. 15) one and a half hours after we settled on the bottom at 305 m on 25 February 1987 at 1845 hours off Cayman. Daylight was still barely visible. When we turned on the lights it swam away and did not return.

Isurus paucus **Guitart Manday, 1966, Longfin Mako—**We were startled to see a male about 275 cm TL make a single, short and fast pass at our bait after the sub had settled on the bottom on 24 April 1987 at 2115 hours EST at Cayman for nearly two hours at 748 m. It appeared to be a mature male; the long claspers and caudal keel were clearly visible. Castro (1983) reports this species has been caught off Cuba as deep as 120 fathoms (219 m) usually by swordfish longlines. Our observation may be a new depth record for *Isurus*.

Apristiurus **sp., Cat Shark—**Four individuals, 30 to 40 cm TL, were seen lying nearly motionless on the bottom in 876-944 m off Cayman on 24 and 25 May 1987. They had dark, almost black bodies, green eyes set far back on the head, and well separated dorsal fins of equal size also set far back along the body.

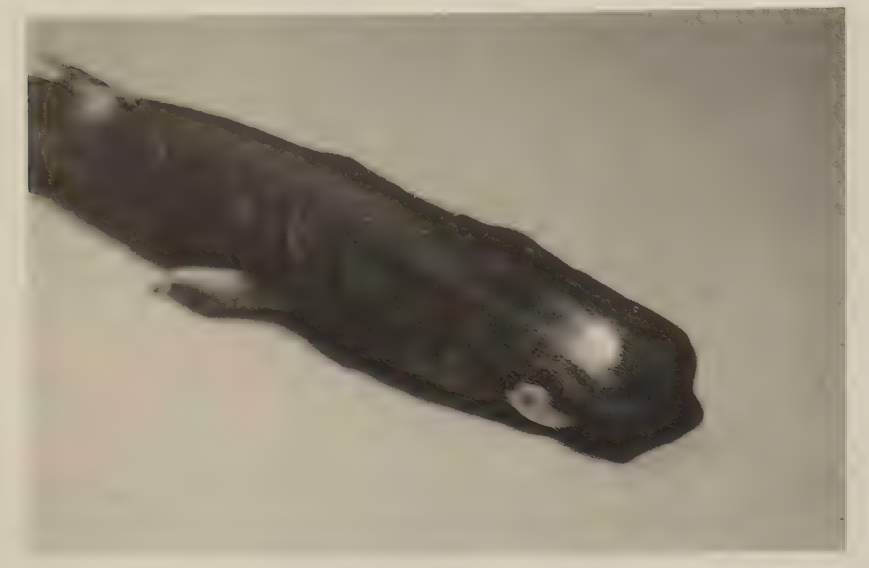

Figure 16.
A preserved specimen of *Etmopterus pusillus*, 20 cm TL, from Japan. A fiber optics light in the mouth shows through the unpigmented skin above the pineal region of the brain. (Photo by Claude E. Petrone.)

Etmopterus pusillus **(Lowe, 1839), Lantern Shark**—One small black shark, 20 cm TL, believed to be *E. pusillus* was observed at 922 m on 27 July 1987 in Bermuda. It had a conspicuous white spot on its head. See pineal window of *Etmopterus* discussed below. In the Bahamas, we observed a small shark at 621 m, apparently of this genus, about 25 cm TL, with a pale body with horizontal lines on its side, and dark spots on its fins. It swam around the bait for over half an hour undisturbed by bright lights.

Miscellaneous Sharks—At least eleven sharks were seen that could not be identified to genus because they were too small or too far away. They may have been scyliorhinid or squaliform sharks and were between 20 and 150 cm TL. They have been included in our total counts (Table 2).

Raja teevani **Bigelow and Schroeder, 1951, Teevan's Skate**—One individual, 85 cm DW, was observed at 305 m on a wide sandy plain at Cayman, 26 April 1987 at 881 m. It approached the bait after the sub was on the bottom for over one hour and stayed for 10 minutes. It was not noticeably disturbed by our lights but did not eat any bait. Our photographs match the color photo and description in Uyeno et al. (1983).

Breviraja colesi **(Bigelow and Schroeder, 1948), Cole's Skate**—One immature male, 14 cm DW was captured November 1987 on the opening of a suction tube and put into a container carried on the *Johnson Sea Link II*. It did not show spots on the dorsal area of each pectoral wing typical of *B. colesi* but otherwise agreed with this species.

Benthobatus marcida **Bean and Weed 1909, Deep-Sea Electric Ray**—Three immature specimens, DW 7–8 cm, were seen and two females were collected in the suction tube of the *Johnson Sea Link II* on 8 November 1987. They were lying far apart on the sand at 564 m.

Narcine **sp. ?**—One small, pale electric ray, DW 20 cm, with no conspicuous marking was swimming just above the sand off Cayman at 305 m depth. It was too far away to see any distinguishing features. It might have been a juvenile of *N. brasiliensis* (Olfers, 1831).

The Pineal Window of Sharks

When we observed the dorsal aspect of these deep-sea sharks, a distinct white spot was noted and/or photographed on the heads of many individuals of *Hexanchus griseus*, most of the *Centrophorus granulosus* and *C. uyato*, and one *Etmopterus pusillus*. (See data and discussions under each species and Figures 4 and 9.)

At the fish collections of the Smithsonian Institution, one of us (EC) examined 4 specimens of *Centrophorus granulosus*, 18 of *C. uyato*, and 2 *C. struhsakeri*. All were adults or nearly of adult size, in good condition in alcohol. All had a noticeable unpigmented pineal window and some degree of countershading. Three adult specimens of *Etmopterus pusillus* over 30 cm TL at the Smithsonian, showed a reduction of scales over the pineal window. This was also evident in 12 *E. brachyurus* and 11 *E. pusillus* from Japan given to one of us (EC) by Hajima Masuda. A fiber optics light placed in the mouth of a 20 cm TL specimen showed through the top of the head over the pineal region (Fig. 16).

Gruber et al. (1975) have demonstrated this ''window to the epiphysis'' in shallow water sharks and Niwa (1983) has shown it to be present in both *E. pusillus* and *E. lucifer*. They conclude that these ''windows'' are median dorsal photoreceptors that would allow sunlight or full moonlight from above to reach the pineal complex. The wide depth range in which we observed numerous specimens of *Hexanchus griseus* and two species of *Centrophorus* (Table 2, Fig. 2) between the disphotic and aphotic zones supports these observations that the pineal window may play a role in mediating vertical diel migrations of some deep-sea sharks. These large predators probably do not need the protection of hiding in aphotic conditions but rather find pineal light reception to be an advantage when seeking prey.

Acknowledgments

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Phylogenetic Interrelationships of Skates: A Working Hypothesis (Chondrichthyes, Rajoidei)

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ABSTRACT

Anatomical information gathered primarily within the last 40 years was used to construct a phylogenetic hypothesis for skates (Chondrichthyes, Rajoidei). A phylogenetic analysis using a parsimony software program (PAUP), constructed of 19 supraspecific taxa (subgenera and genera level taxa) and 34 characters, revealed 45 most parsimonious trees with a consistency index of 0.565 and a tree length of 62. These trees were subjected to a strict consensus tree analysis which produced a single tree. The consensus tree consisted of two familial level assemblages (Group I and Group II). *Atlantoraja*, representing *Raja* (*Atlantoraja*) and *R.* (*Rioraja*), was the sister group of the two major clades of Group I. One of the major clades consisted of *Bathyraja* and its sister group, *Arhynchobatis* and *Psammobatis* plus *Sympterygia*. The other major clade consisted of *Notoraja* and its sister group, Subgenus A and its sister group, *Irolita*, *Pseudoraja*, and *Pavoraja*. Group II consisted of four major clades with unresolved affinities, *Cruriraja* and *Anacanthobatis*; *Raja* (*Dipturus*), *R.* (*Okamejei*), *R.* (*Raja*), *R.* (*Rostroraja*), a North Pacific *Raja* assemblage, and an amphi-American *Raja* assemblage; *Raja* (*Amblyraja*), *R.* (*Leucoraja*), *R.* (*Rajella*), *Breviraja*, and *Dactylobatus*; and *Raja* (*Malacoraja*), *Neoraja*, *Gurgesiella* (*Fenestraja*), and *G.* (*Gurgesiella*). The analysis indicates that skates consist of two family level taxa, that the genus *Raja* is polyphyletic and that the genus *Pavoraja* is paraphyletic. It also reveals that there are wide scale character state parallelisms and reversals in Rajoidei, which may have caused the low consistency index and partial disagreement of this parsimony analysis. Further research is needed to elucidate the relationships, particularly of *Irolita*, *Pseudoraja*, and *Pavoraja*, and to clarify the status of *Bathyraja* and *Rhinoraja*.

Introduction

Skates (Rajoidei) comprise the largest putative monophyletic subordinal level taxon of the chondrichthyans. Currently there are about 224 to 227 nominal species and as many as 20 undescribed species in collections around the world. Within the last 40 years there has been great interest in the systematics and phylogenetics of skates and, to a lesser extent, other batoids (sawfishes, guitarfishes, electric rays, and stingrays). Over one-half of the currently recognized species of skates have been described within the last 40 years. Regional systematic studies have largely solved the systematic problems in the northwestern Pacific (Ishiyama 1958, 1967; Chan 1965a, b; Ishiyama and Ishihara 1977; Zhu et al. 1981; Deng et al. 1983; Dolganov 1983, 1985b; Ishihara and Ishiyama 1985, 1986; Ishihara 1987; Stehmann In press); the northwestern Atlantic (Bigelow and Schroeder 1948, 1950, 1951a, b, 1953, 1954a, b, 1958, 1962, 1964, 1965a, b, 1968a, b; McEachran and Martin 1978; McEachran 1977; McEachran and Compagno 1982; McEachran and Matheson 1985; McEachran and Miyake 1987; McEachran and Stehmann 1977, 1984); the northeastern Atlantic (Stehmann 1970, 1973, 1976b, 1977, 1978a; Hulley and Stehmann 1977; Stehmann and Bürkel 1984; Dolganov 1985a; McEachran et al. 1989); the tropical eastern Atlantic (Krefft 1965; Stehmann 1971a, c; Capape 1977a, b; Stehmann and Seret 1983); the southeastern Atlantic and southwestern Indian Ocean (Hulley 1966, 1969, 1970, 1972a, c, 1973, 1986; Wallace 1967; McEachran et al. 1989); the southwestern Atlantic (Menni 1971, 1972a, b, 1973; Krefft 1968; Stehmann 1971b, 1978b, 1985a; Krefft and Stehmann 1974, 1975; Sadowski and Menni 1974; Figueiredo 1977; Roux 1977; McEachran and Compagno 1980; McEachran 1982, 1983); the northern Indian Ocean (Stehmann 1976a; McEachran and Fechhelm 1982a, b; Seret 1986a, b); the southeastern Pacific (Chirichigno 1968, 1974; McEachran 1982, 1983; McEachran and Miyake 1984, 1986; Perqueno and Lamilla 1985); the Antarctic (Bigelow and Schroeder 1965a; Springer 1971; Stehmann 1985b); and the northeastern Pacific (Ishihara and Ishiyama 1985, 1986; Dolganov 1983, McEachran and Miyake 1986, 1988). The skate fauna of the southwestern Pacific has been only partially studied (Garrick 1954, 1957, 1961; Garrick and Paul 1974; Dolganov 1985c; Last In press).

These regional studies have been largely successful in grouping skates into supraspecific taxa (subgenera and genera), although in most cases, they have not dealt with all of the species within a supraspecific taxon. Thus supraspecific taxa have frequently been defined with inadequate data bases and a number of taxa, i.e., *Bathyraja*, *Rhinoraja*, *Raja*, *R.* (*Dipturus*), *R.* (*Rostroraja*), are probably either paraphyletic or polyphyletic.

Ishiyama (1958) erected two subgenera (*Okamejei* and *Tenugei*) for *Raja* and three subgenera (*Arctoraja*, *Bathyraja*, and *Notoraja*) for *Breviraja*. Ishiyama and Hubbs (1968) removed the above three subgenera from *Breviraja* and placed them as subgenera in *Bathyraja*. Stehmann (1970) erected six subgenera (*Amblyraja*, *Dipturus*, *Leucoraja*, *Malacoraja*, *Raja*, and *Rajella*) for the genus *Raja* and synonymized *Tenugei* with *Dipturus*. Hulley (1972a) erected the subgenus *Rostroraja* within the genus *Raja*. Menni (1972a) erected two subgenera (*Atlantoraja* and *Rioraja*) for *Raja*. Hulley (1973) discussed the interrelationships within Anacanthobatidae although he lacked material on several of the species and three species were described subsequent to his study. Hulley (1972b) and McEachran and Compagno (1979) discussed the interrelationships of Gurgesiellidae and Pseudorajidae. McEachran and Compagno (1980) described a new species of *Gurgesiella* and elucidated the interrelationships of the three species within the genus. McEachran and Compagno (1982) split the genus *Neoraja* from *Breviraja*, erected two subgenera (*Neoraja* and *Fenestraja*) for *Neoraja* and elucidated the interspecific interrelationships within *Neoraja*. McEachran (1984) removed *Fenestraja* from *Neoraja* and placed it as a subgenus of *Gurgesiella*, erected the tribe Pavorajini for the supraspecific taxa *Malacoraja*, *Neoraja*, *Pavoraja*, Subgenus A, and *Gurgesiella* and elucidated the interrelationships among these supraspecific taxa. McEachran and Matheson (1985) and McEachran and Miyake (1987) elucidated the interrelationships of *Breviraja*. McEachran (1982, 1983) revised the genera *Sympterygia* and *Psammobatis* and elucidated the interspecific relationships within each of the genera. McEachran and Miyake (1986) erected the tribe Rajini for the supraspecific taxa *Raja* (*Dipturus*), *R.* (*Okamejei*), *R.* (*Raja*), and *R.* (*Rostroraja*), a North Pacific *Raja* assemblage and an amphi-American *Raja* assemblage. Stehmann (In press) removed *Notoraja* from *Bathyraja* and elevated it to generic status. McEachran and Fechhelm (1982a) resurrected *Pavoraja* from synonymy with the genus *Raja*.

Several authors have proposed phylogenetic hypotheses for Rajoidei (Ishiyama 1958, 1967; Stehmann 1970; Hulley 1972a, 1973; McEachran 1984). However, the first three authors based their studies on regional skate faunal revisions and thus dealt with only a subset of the variation within Rajoidei. Ishiyama dealt with the skate fauna of the western North Pacific. This fauna represents four of the currently recognized 29 supraspecific taxa. Stehmann treated the skate fauna of the eastern North Atlantic, which contains seven supraspecific taxa. Both Ishiyama and Stehmann placed all of the skate taxa in the family Rajidae. Hulley (1972a, b, c, 1973) investigated components of 10 supraspecific taxa from the southern African region and an additional one from the western North Atlantic. He recognized four families of skates, Anacanthobatidae, Crurirajidae, Gurgesiellidae, and Pseudorajidae, in addition to Rajidae. McEachran included 21 supraspecific taxa in his study and recognized two family level taxa. The studies of Ishiyama, Stehmann and Hulley did not distinguish between derived (apomorphic) and primitive (plesiomorphic) character states. This resulted in the recognition of mutually exclusive dichotomous groups. The one possessing the derived character state can be considered a putative monophyletic group while the one possessing the primitive state can not be considered a monophyletic group. The latter study (McEachran 1984) was based on a worldwide but insufficient survey of skate taxa and will be dealt with in the present study.

Further progress in elucidating the systematics and phylogenetics of Rajoidei will entail extending the species level revisions to the remaining untreated supraspecific taxa, using these analyses to further resolve the interrelationships among supraspecific taxa of Rajoidei and finally using all of these analyses to hypothesize the interrelationships of skates with the other batoids.

The purposes of the present study are to construct a working hypothesis of the interrelationships (cladogram) of Rajoidei based on the results of the above studies and data collected subsequent to these studies, and to use this hypothesis to indicate taxonomic areas within Rajoidei which are in need of further investigation. Areas of this cladogram which lack resolution or which are incongruent can then be subjected to more detailed examination and the data thus gathered used to further test and refine the working hypothesis.

Materials and Methods

Data used in this study were either obtained from the above studies or from specimens examined by the senior author. Acronyms for institutions housing the specimens used and cited in this study follow Leviton et al. (1985). Specimens of all of the supraspecific taxa of skates and from as many species as possible were measured according to Bigelow and Schroeder (1953) and McEachran and Stehmann (1984); radiographed to count vertebrae and pectoral and pelvic radials; and dissected to reveal the structure of the neurocranium, hypobranchial skeleton, scapulocoracoid, and

Table 1.
Characters and character states of rajoid supraspecific taxa used in PAUP analysis.

Characters	Character states
1 Scapulocoracoid	0 stout anterior bridge, 1 slender anterior bridge, 2 without anterior bridge
2 Scapulocoracoid	0 postdorsal foramina, 1 with postdorsal fenestra
3 Basihyal	0 without lateral projections, 1 with lateral projections
4 Ventral terminal cartilage	0 not spoon-shaped, 1 spoon-shaped
5 Dorsal terminal 2 and 3 cartilages	0 arranged in series, 1 arranged in parallel
6 Preorbital process	0 without flange, 1 with flange
7 Propterygia of pectoral	0 falling short of rostral note, 1 reaching girdle rostral node
8 Clasper glans	0 without projection, 1 with projection
9 Rostral shaft	0 stout medially, 1 slender over entire length
10 Anterior fontanelle	0 narrow extending on to rostrum, 1 oval and extending little beyond nasal capsules
11 Rostral shaft	0 unsegmented at base, 1 segmented at base
12 Clasper glans	0 without rhipidion, 1 with rhipidion
13 Dorsal terminal 1 cartilage	0 present, 1 absent
14 Nasal capsules	0 without basal fenestrae, 1 with basal fenestrae
15 Internasal plate	0 broad, 1 narrow
16 Nasal capsules	0 narrow, 1 broad and oval-shaped
17 Rostral appendices	0 abutting against rostral shaft or separated from rostral shaft and plate-like, 1 separated from rostral shaft and narrow
18 Posterior section of rostral appendices	0 flat, oval in cross section
19 Rostral shaft	Continuous with rostral node, 1 separate from rostral node
20 Clasper glans	0 little expandable, 1 greatly expandable
21 Clasper glans	0 without shield, 1 with shield
22 Pelvic girdle	0 anterior and posterior lobes continuous, 1 lobes separate
23 Pelvic girdle	0 radials present on proximal aspect of metapterygium, 1 radials absent on proximal aspect of metapterygium
24 Clasper glans	0 with eperon, 1 without eperon
25 Clasper skeleton	0 ventral terminal and accessory terminal 1 cartilages not connected, 1 ventral terminal, and accessory terminal 1 cartilages connected
26 Scapulocoracoid	0 with postventral foramina, 1 with expanded postventral fenestra
27 Accessory terminal 1 cartilage	0 with slender tip, with expanded tip
28 Accessory terminal 1 cartilage	0 without well developed proximal arms, 1 with well developed proximal arms
29 Rostral appendices	0 oval in cross section or flattened and abutting against rostral shaft, 1 flattened and separated from rostral shaft
30 Dorsal marginal cartilage	0 with distal extension, 1 without distal extension
31 Ventral terminal cartilage	0 without mediolateral expansion, 1 with mediolateral expansion
32 Preorbital process	0 moderate to well-developed, 1 degenerate
33 Ventral terminal cartilage	0 not check- or J-shaped, check- or J-shaped
34 Nasal capsules	0 located lateral to precerebral space, 1 bulging into precerebral space

clasper. Embryos of species of several supraspecific taxa were cleared and double stained (Dingerkus and Uhler 1977) to elucidate ontogenetic development.

The data set generated from the anatomical survey was subjected to a comparative phylogenetic analysis (Hennig 1966) as outlined by Eldredge and Cracraft (1980) and Wiley (1981). Character polarities were assessed by the outgroup method (Watrous and Wheeler 1981; Maddison et al. 1984). When appropriate, the ontogenetic method was integrated with the outgroup method for assessing polarities and homologies as outlined by Fink (1982) and recommended by Alberch (1985).

The working hypothesis was generated with a phylogenetic analysis using parsimony (PAUP, version 2.40) (Swofford 1986). The 29 supraspecific taxa recognized in this study were condensed to 19 taxa plus the outgroup (*Rhinobatos*). The 29 supraspecific taxa consist of all of the nominal subgenera of *Gurgesiella*, *Pavoraja*, and *Raja*, and all the genera of Rajoidei. Pairs of supraspecific taxa that shared complex derived character states and thus were thought, with high likelihood, to be sister groups were combined into a single taxon to facilitate the analysis. The data matrix consisted of 20 supraspecific taxa (OTUs) and 34 characters (Tables 1, 2). The characters chosen were those which varied among the taxa and in which the derived character state was, in nearly all cases, shared by two or more but less than 20 of the taxa. All character states were coded as present or absent, except for the anterior bridge of the scapulocoracoid which was recorded as present, present but very slender, or absent. Claspers of *Pseudoraja* were unavailable for study because no mature males exist in research collections; thus, all clasper character states of

Table 2.
Character matrix used in the PAUP analysis.

Taxon	Character state
Atlantoraja	1111190000000000000000000000000000
Bathyraja	0110011100000000000000000100001000
Arhynchobatis	0110011110100000000000000100011000
Psammobatis	0110091110000000000000000100100000
Irolita	1111011110100000000000010111111010
Pseudoraja	1191091019990000990990110110199910
Notoraja	1111010000000000000000110110101010
Subgenus A	2111010000100000000000110110111010
Pavoraja	2111011010100000000000110190101010
Cruriraja	2001000001111000000000000000000001
Anacanthobatis	2001000001111000000001000000000001
Dipturus	2001000001110111000000000000000000
Okamejei	2001000001110111110000000000000000
Raja	2001000001010111100000000000000000
Leucoraja	2000000001110000011100000000000000
Breviraja	2000000001110000001110000100000000
Malacoraja	2000000001110000000001111000000000
Fenestraja	2001000001110000000001111111110110
Gurgesiella	2001000001110000000001111111110110
Rhinobatos	0000000000000000000000000000000000

0 = plesiomorphic state
1, 2 = apomorphic state
9 = unknown state

Pseudoraja were recorded as unknown. The tree was rooted to the putative sister group (ancestor), *Rhinobatos*.

Rhinobatos was selected as the outgroup because Rhinobatoidei is considered the sister group of Rajoidei (Miyake and McEachran In press) and *Rhinobatos* is considered to be the most primitive supraspecific taxon of Rhinobatoidei (K. Nishida, ASIH Annu. Meeting, Ann Arbor, MI, pers. commun., June 1988). Inclusion of additional outgroups in the analysis would have added to the credibility of the polarity decisions but this was not done because of lack of knowledge of characters states and perceived specializations of other potential outgroup taxa, i.e., torpedinoids, pristoids, pristiophoroids, and squatinoids.

Results

The phylogenetic analysis (PAUP) revealed the 45 most parsimonious trees with a consistency index of 0.565 and a tree length of 62. These trees were subjected to a strict consensus tree analysis which produced a single tree resolved to the lowest level possible given the relationships expressed in the most parsimonious trees (Fig. 1). The strict consensus tree had a Mickevich's (1978) consensus information of 0.500 and contained 26 synapomorphies and 36 homoplasies (8 reversals and 28 parallelisms).

Figure 1.
Strict consensus tree of Rajoidei. Numbers correspond to numbers of characters in Table 1 and to numbers of character states in text. Numbers to the right of the vertical lines represent synapomorphies and parallelisms, and numbers to the left of the lines represent reversals.

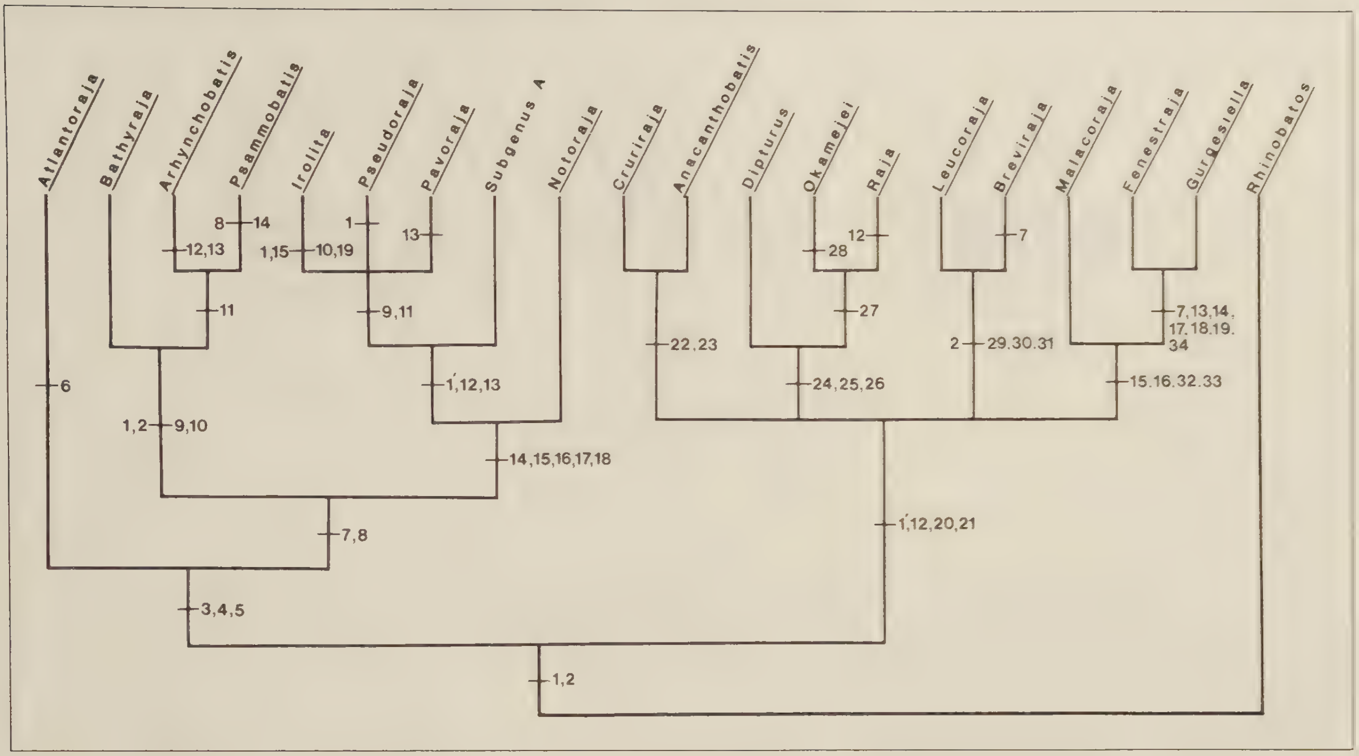
Figure 2.
Empirically derived cladogram of Rajoidei adapted from McEachran (1984).

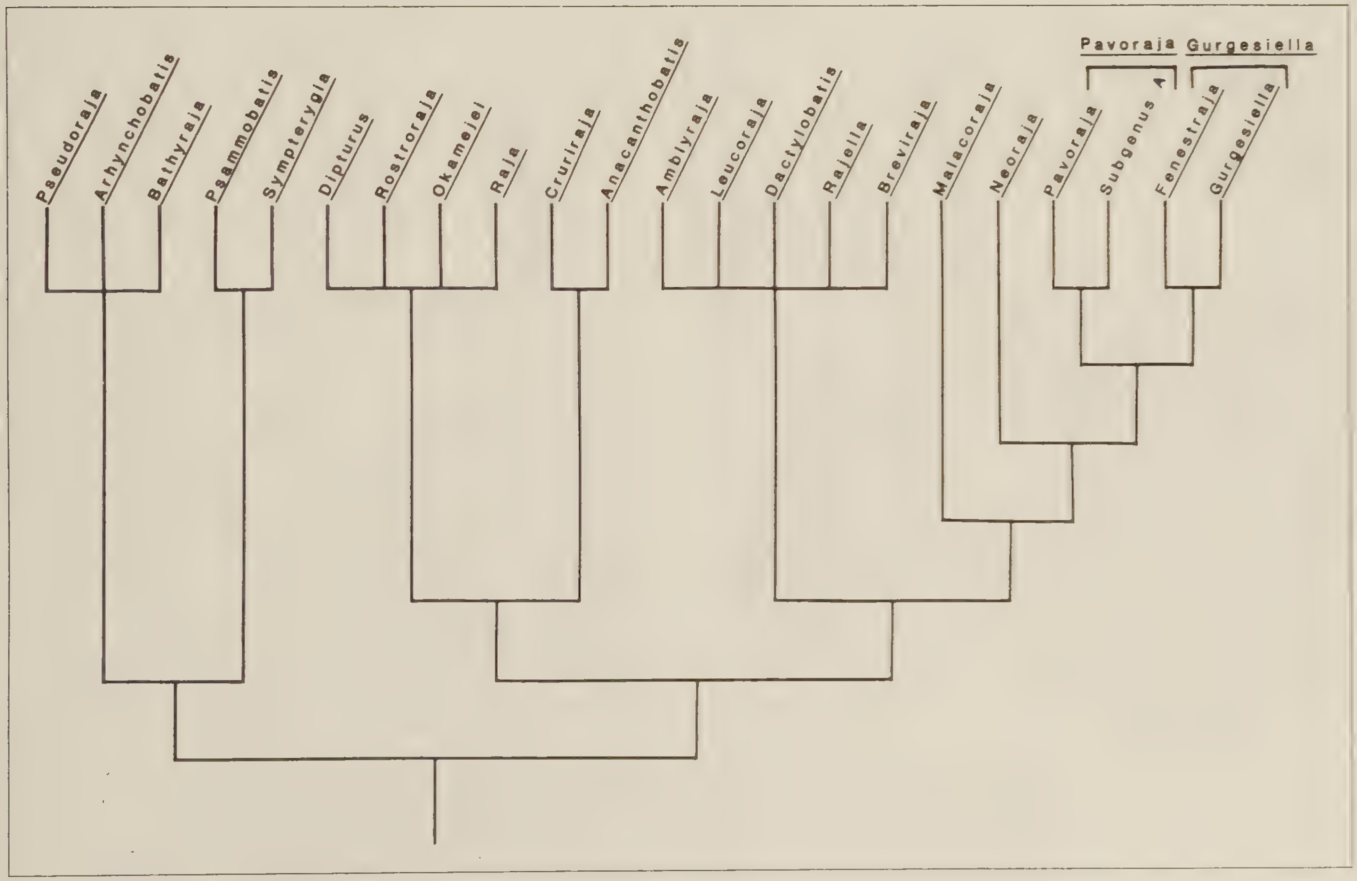
Basally the supraspecific taxa were arranged into two assemblages of 9 and 10 supraspecific taxa, provisionally called Group I and Group II respectively. The strict consensus tree has the same topology as an empirically derived phylogenetic hypothesis of Rajoidei (McEachran 1984) except for placement of two supraspecific taxa (Fig. 2). *Pavoraja* and Subgenus A are placed in Group II in McEachran (1984) but are consistently placed in Group I in the strict consensus tree and in the 45 most parsimonious trees.

In the strict consensus tree, Group I has three synapomorphies: basihyal cartilage of the gill arch skeleton with laterally directed projections (3) (Fig. 3); claspers with a spoon-shaped ventral terminal cartilage (4) (Fig. 4); and dorsal and ventral terminal 2 and 3 clasper cartilages arranged in parallel (5). The basihyal lacks lateral projections in *Rhinobatos* and in Group II. In Rhinobatos the ventral terminal cartilage is differently shaped (Ishiyama 1958; Hulley 1972a) and is associated with the axial cartilage rather than with the ventral marginal and accessory terminal 1 cartilages and thus may be homologous with the accessory terminal 2 cartilage rather than with the ventral terminal cartilage of skates. Some galeomorph sharks have a cartilage (TV2 or RV2 of Compagno 1988) which may be homologous with the ventral terminal cartilage of skates, but this cartilage is differently shaped from that in Group I. The ventral terminal cartilage of Group II is not spoon-shaped and possesses a sharp lateral edge, forming the component shield (Ishiyama 1958; Stehmann 1970; Hulley 1972a; Ishihara 1987). In *Rhinobatos* and Group II the dorsal terminal 2 and 3 cartilages are arranged in series (Ishiyama 1958; Stehmann 1970; Hulley 1972a; Ishihara 1987).

Atlantoraja is the sister group of the remainder of Group I and is thought to comprise the western South Atlantic taxa, *Raja* (*Atlantoraja*) (three species) and *R.* (*Rioraja*) (one species). This clade possesses one synapomorphy, presence of a flange extending from the preorbital process to the supraorbital crest (6) (Fig. 5). Neither *Rhinobatos* nor other rajoids possess this flange.

The remaining eight supraspecific taxa share a derived character, propterygium of the pectoral girdle reaching the rostral node (7), and a synapomorphy, clasper glans with the component projection (8). Propterygia which reach the


Atlantoraja
Bathyraja
Arhynchobatis
Psammobatis
Irolita
Pseudoraja
Pavoraja
Subgenus A
Notoraja
Cruriraja
Anacanthobatis
Dipturus
Okamejei
Raja
Leucoraja
Breviraja
Malacoraja
Fenestraja
Gurgesiella
Rhinobatos
8
14
12,13
11
1
1,15
10,19
13
9,11
12
28
27
7
22.23
2
29.30.31
7,13,14.
17.18.19.
34
6
1′,12,13
24,25,26
15.16.32.33
1,2
9,10
14,15,16,17,18
1′,12,20,21
7,8
3,4,5
1,2


Pavoraja
Gurgesiella
Pseudoraja
Arhynchobatis
Bathyraja
Psammobatis
Sympterygia
Dipturus
Rostroraja
Okamejei
Raja
Cruriraja
Anacanthobatis
Amblyraja
Leucoraja
Dactylobatis
Rajella
Breviraja
Malacoraja
Neoraja
Pavoraja
Subgenus A
Fenestraja
Gurgesiella

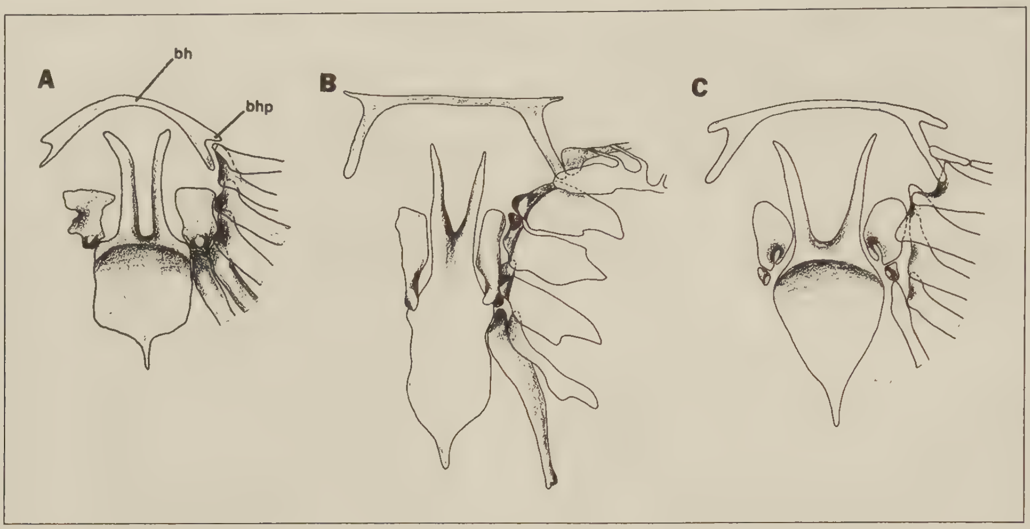


Figure 3.
Ventral gill arch skeleton of Group I. A, *Raja* (*Atlantoraja*) *cyclophora* TCWC 3696.1; B, *Sympterygia brevicaudata* CAS (SU 13897); C, *Pseudoraja fischeri* USNM uncat. bh = basihyal cartilage, bhp = lateral process on basihyal cartilage.

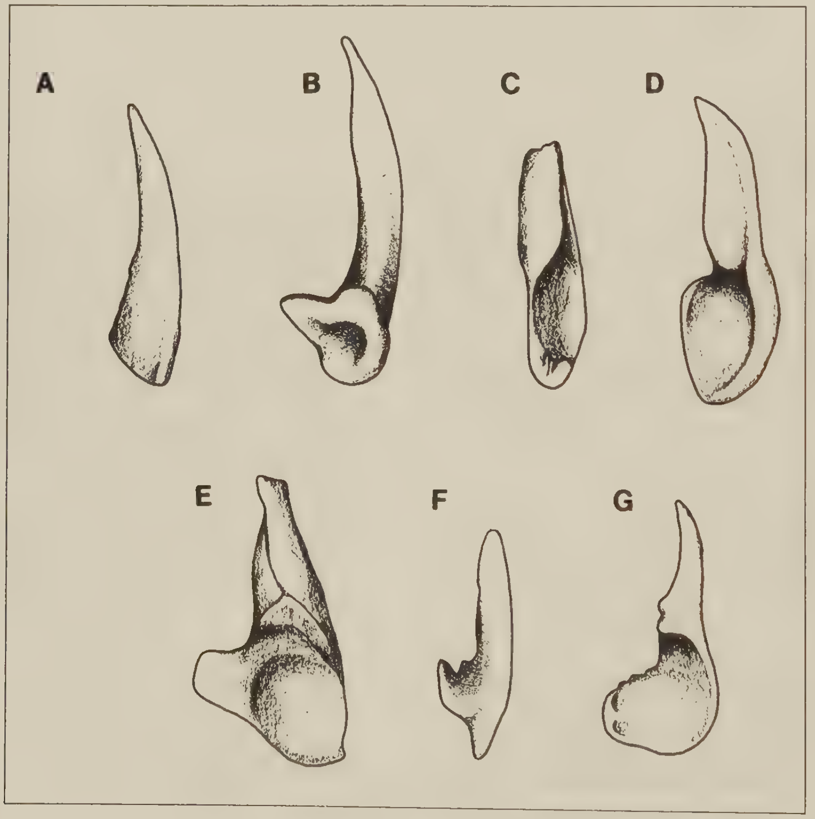


Figure 4.
Dorsal view of ventral terminal clasper cartilage of Group I. A, *Bathyraja* sp. MTUF 21889; B, *Arhynchobatis asperrimus* NMNZ 5200; C, *Psammobatis bergi* CAS (SU 14034); D, *Irolita waiti* WAM P702; E, *Notoraja tobitukai* MCZ 40268; F, *Pavoraja* (Pavoraja) *alleni* WAM P19118; G, *Pavoraja* (Subgenus A) *asperula* NMNZ 5697.

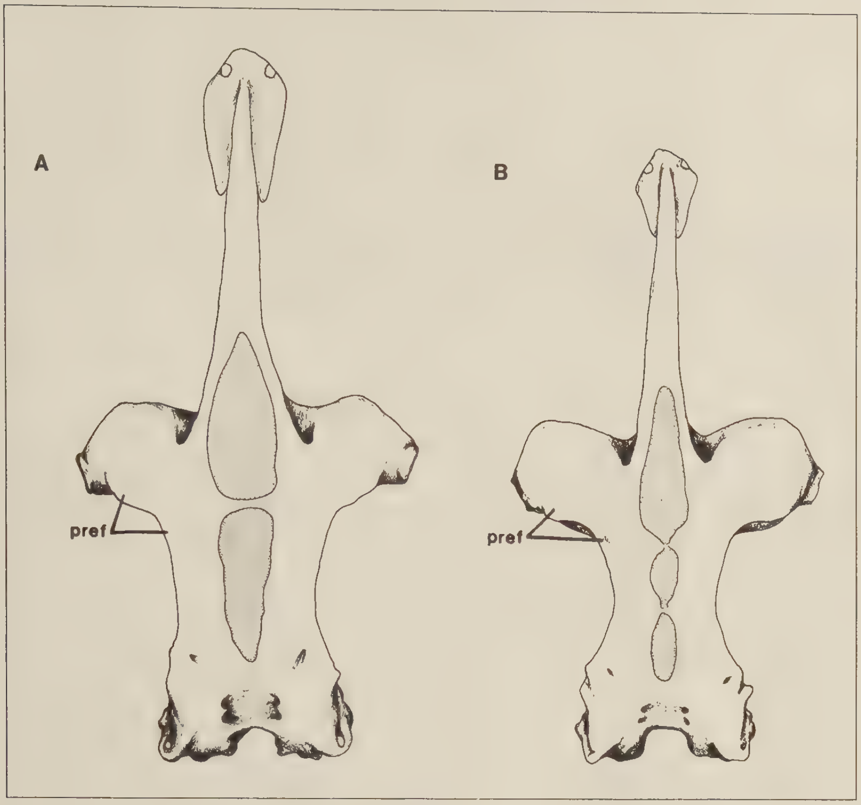


Figure 5.
Dorsal view of neurocrania. A, *Raja* (*Rioraja*) *agassizi* TCWC uncat. B, *Raja* (Atlantoraja) *cyclophora* TCWC 3696.1. pref = preorbital flange.

rostral node have evolved separately in *Breviraja* and in *Fenestraja* and *Gurgesiella* of Group II. The component projection results from fusion of the accessory terminal 1 cartilage with the ventral marginal cartilage (McEachran 1983). Fusion of this cartilage is thought to be derived because the accessory terminal 1 exists as a separate cartilage in *Rhinobatos* and *Atlantoraja* (Ishiyama 1958; Hulley 1972a; Menni 1973).

The eight taxon clade is subdivided into two clades of three and five supraspecific taxa. The three taxon clade of *Bathyraja*, *Arhynchobatis*, and *Psammobatis* is equivocal in that it is defined by two reversals and two parallelisms. Scapulocoracoids with a stout anterior bridge (1) and with one or more postdorsal foramina (2) are considered reversals because rajoids are defined by two synapomorphies, scapulocoracoids with a slender anterior bridge (1) and a postdorsal fenestra (2), and *Atlantoraja* possesses a slender anterior bridge and a postdorsal fenestra. Group II possesses no anterior bridge and, with the exception of *Leucoraja* and *Breviraja*, possesses a postdorsal fenestra. The parallelism, rostral shaft slender and of about equal width over entire length (9), also occurs in *Irolita*, *Pseudoraja*, and *Pavoraja*. In *Pseudoraja* and *Pavoraja*, the rostral shaft is separated from the rostral base. The other parallelism, anterior fontanelle broad and extending little beyond leading edge of the nasal capsules (10) (Fig. 6), also occurs in *Irolita*. These character states are considered derived because *Rhinobatos* has a stout rostral shaft and narrow anterior fontanelle which extends to near the tip of the rostral shaft as a narrow groove (el-Toubi and Hamdy 1959; Compagno 1977), and *Atlantoraja*, *Notoraja*, and Subgenus A possess moderately stout rostral shafts, which are attenuated anteriorly, and narrow anterior fontanelles which extend on to the rostral shaft (Figs. 5, 6) (Ishiyama 1967; McEachran 1984).

Bathyraja, with 45 species, is the sister group of the *Arhynchobatis* and *Psammobatis* clade. No synapomorphies have been discovered for *Bathyraja*. *Rhinoraja* is combined with *Bathyraja* in the analysis, despite the fact that the four species of this taxon possess a basally segmented rostral shaft (Ishiyama 1958, 1967), because *Rhinoraja* is presently considered to be paraphyletic. If it is later judged to be monophyletic, it will be placed in the *Arhynchobatis* and *Psammobatis* clade which is defined by possession of a basally segmented rostral shaft (11). The basally segmented rostral shaft is considered a parallelism because it also is found in the clade of *Irolita*, *Pseudoraja*, and *Pavoraja*.

Arhynchobatis is monotypic, endemic to New Zealand, and defined by two parallelisms, presence of an erectile tissue (rhipidion) in the clasper glans (12) and absence of the dorsal terminal 1 clasper cartilage (13). Rhipidia are also possessed by the Subgenus A, the *Irolita*, *Pseudoraja*, and *Pavoraja* clade (Fig. 7) and Group II. The dorsal terminal 1 cartilage is also missing in the Subgenus A, *Irolita*, *Pseudoraja*, and *Pavoraja* clade, and in the *Fenestraja* and *Gurgesiella* clade of Group II.

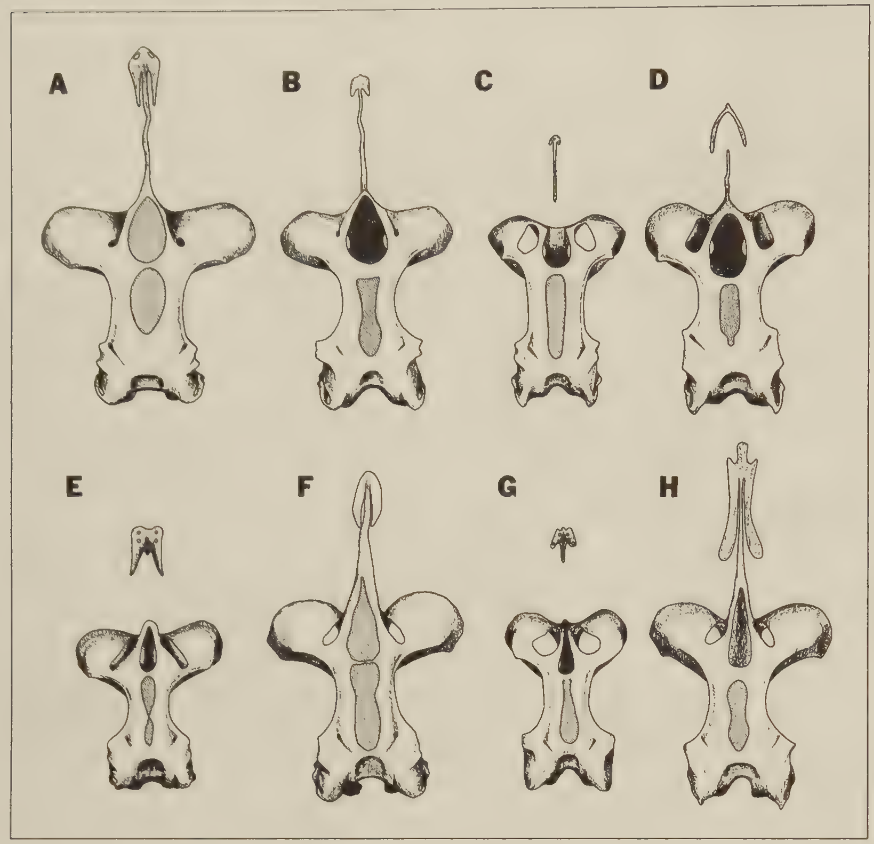


Figure 6.
Dorsal view of neurocrania. A, *Bathyraja peruana* USNM 267045; B, *Arhynchobatis asperrimus* NMNZ 5200; C, *Psammobatis scobina* TCWC uncat.; D, *Irolita waiti* WAM P702; E, *Pseudoraja fischeri* TCWC uncat.; F, *Notoraja tobitukai* MCZ 40284; G, *Pavoraja* (*Pavoraja*) *nitida* WAM B1.5275; H, *Pavoraja* (Subgenus A) *asperula* NMNZ 5697.

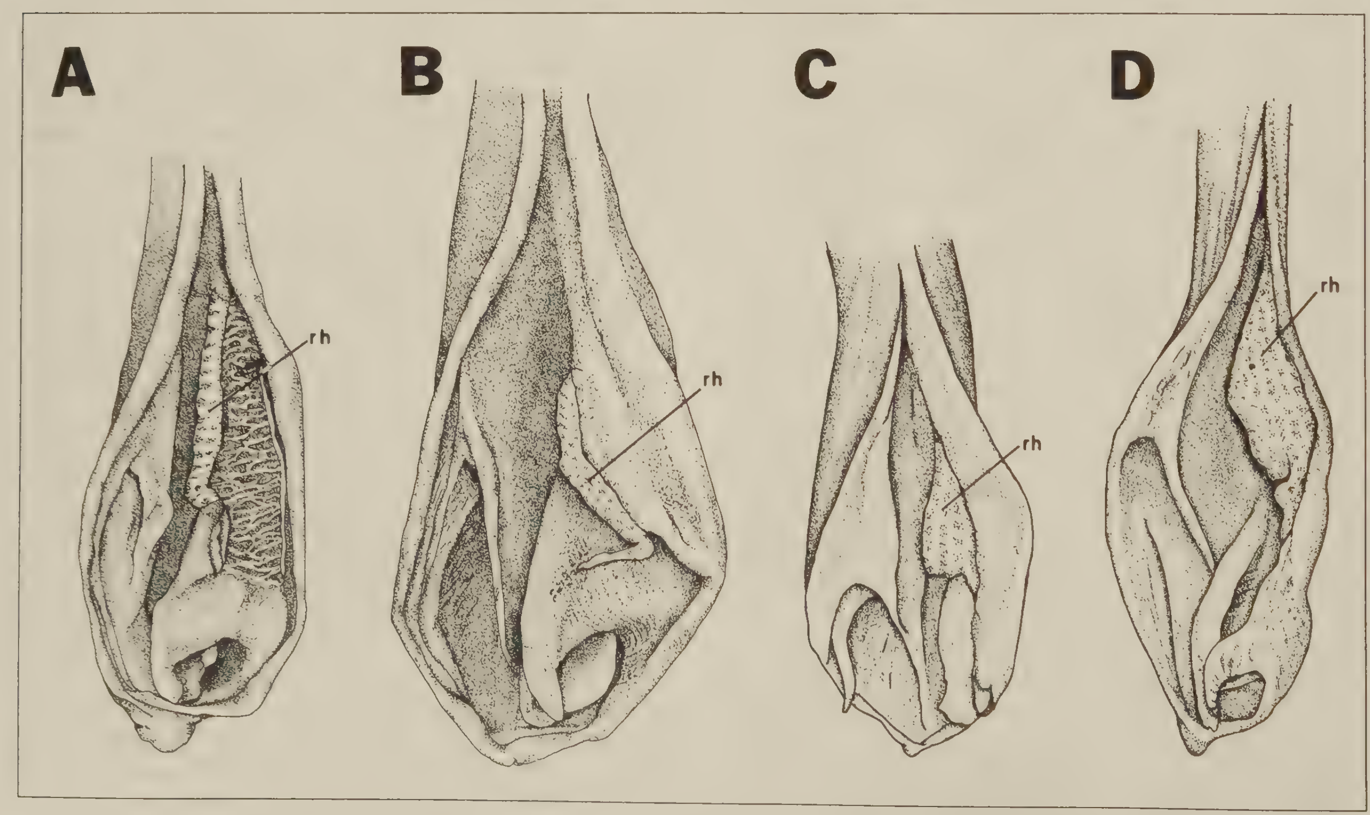


Figure 7.
Lateral view of clasper glans, partially expanded. A, *Arhynchobatis asperrimus* NMNZ 5200; B, *Irolita waiti* WAM P702; C, *Pavoraja* (*Pavoraja*) *nitida* AMS 1B.5275; D, *Pavoraja* (Subgenus A) *asperula* NMNZ 5697. rh = rhipidion.

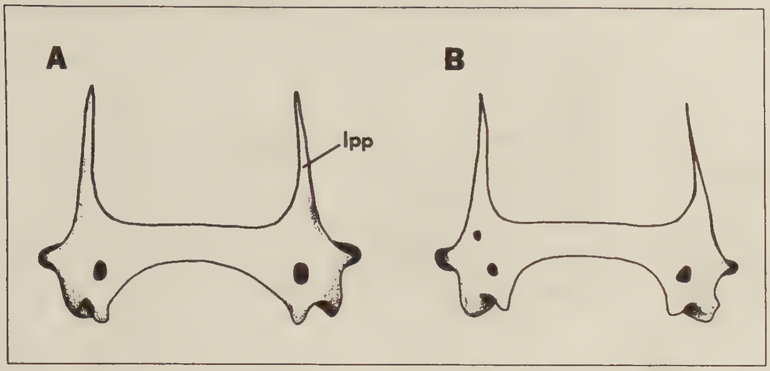


Figure 8.
Dorsal view of pelvic girdles. A, *Psammobatis scobina* TCWC uncat.; B, *Sympterygia brevicaudata* USNM 77710. lpp = lateral prepelvic process.

Psammobatis is defined by a reversal, loss of the clasper component projection (8) (McEachran 1983), and by a parallelism, nasal capsules with a basal fenestra (14). Absence of a projection is considered a reversal because it is present in all of the taxa of Group I except *Atlantoraja* and *Psammobatis*. Basal fenestrae also occur in the *Notoraja*, Subgenus A, *Irolita*, and *Pseudoraja* clade, and the *Fenestraja* and *Gurgesiella* clade of Group II. *Sympterygia* is the sister group of *Psammobatis* (McEachran 1983) and is combined with it in the analysis. The two genera share one synapomorphy, extremely long lateral prepelvic processes (Fig. 8); however, *Sympterygia* lacks a basal fenestra on the nasal

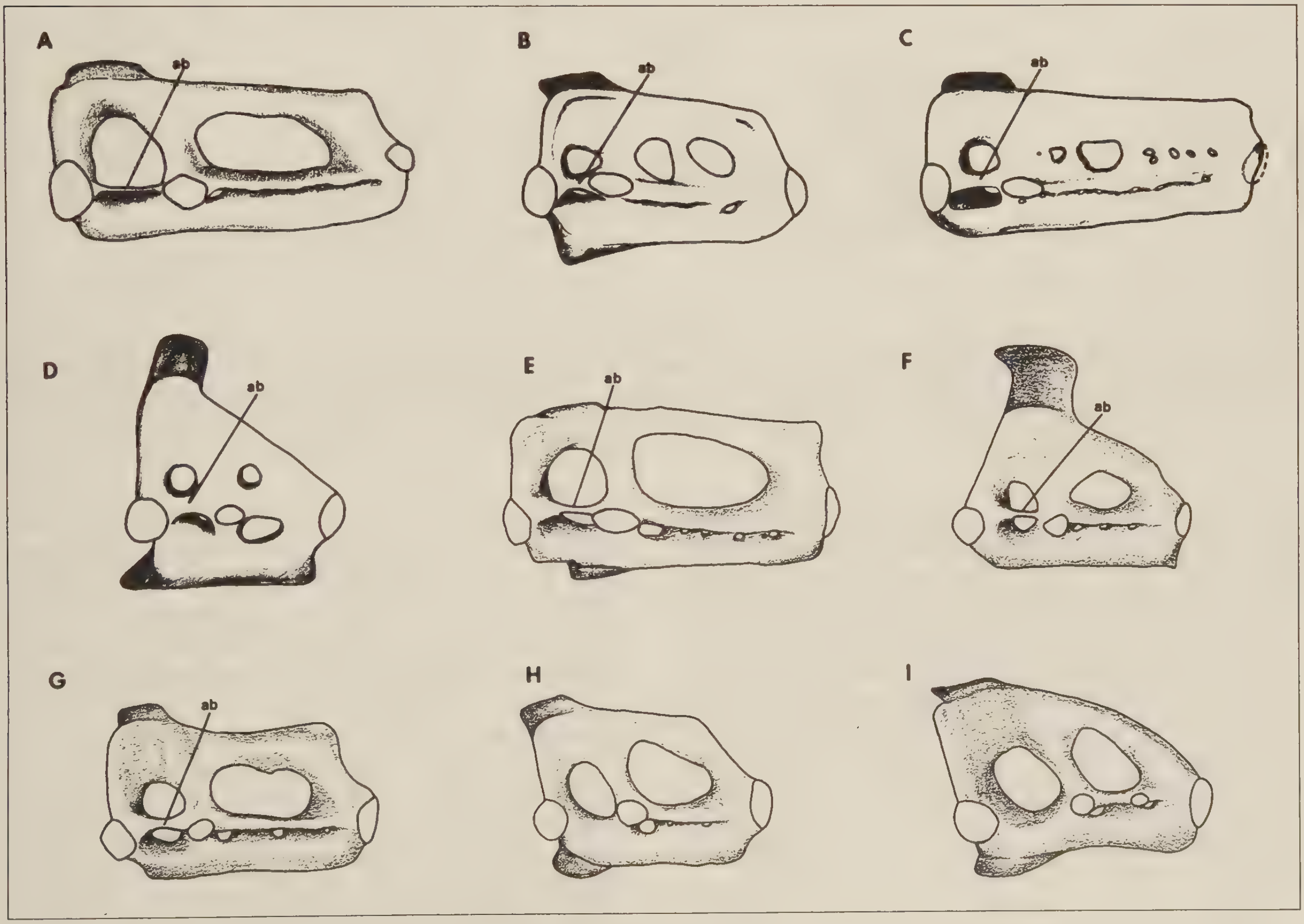


Figure 9.
Lateral view of scapulocoracoids of Group I. A, *Raja* (*Atlantoraja*) *castelnaui* MNHN A8008; B, *Bathyraja interrupta* S10 61-495; C, *Arhynchobatis asperrimus* NMNZ 5200; D, *Psammobatis normani* ISH 1449/56; E, *Irolita waiti* WAM P702; F, *Pseudoraja fischeri* TCWC uncat.; G, *Notoraja tobitukai* MCZ 40284; H, *Pavoraja* (*Pavoraja*) *nitida* AMS 1B.5275; I, *Pavoraja* (Subgenus A) *asperula*. ab = anterior bridge.

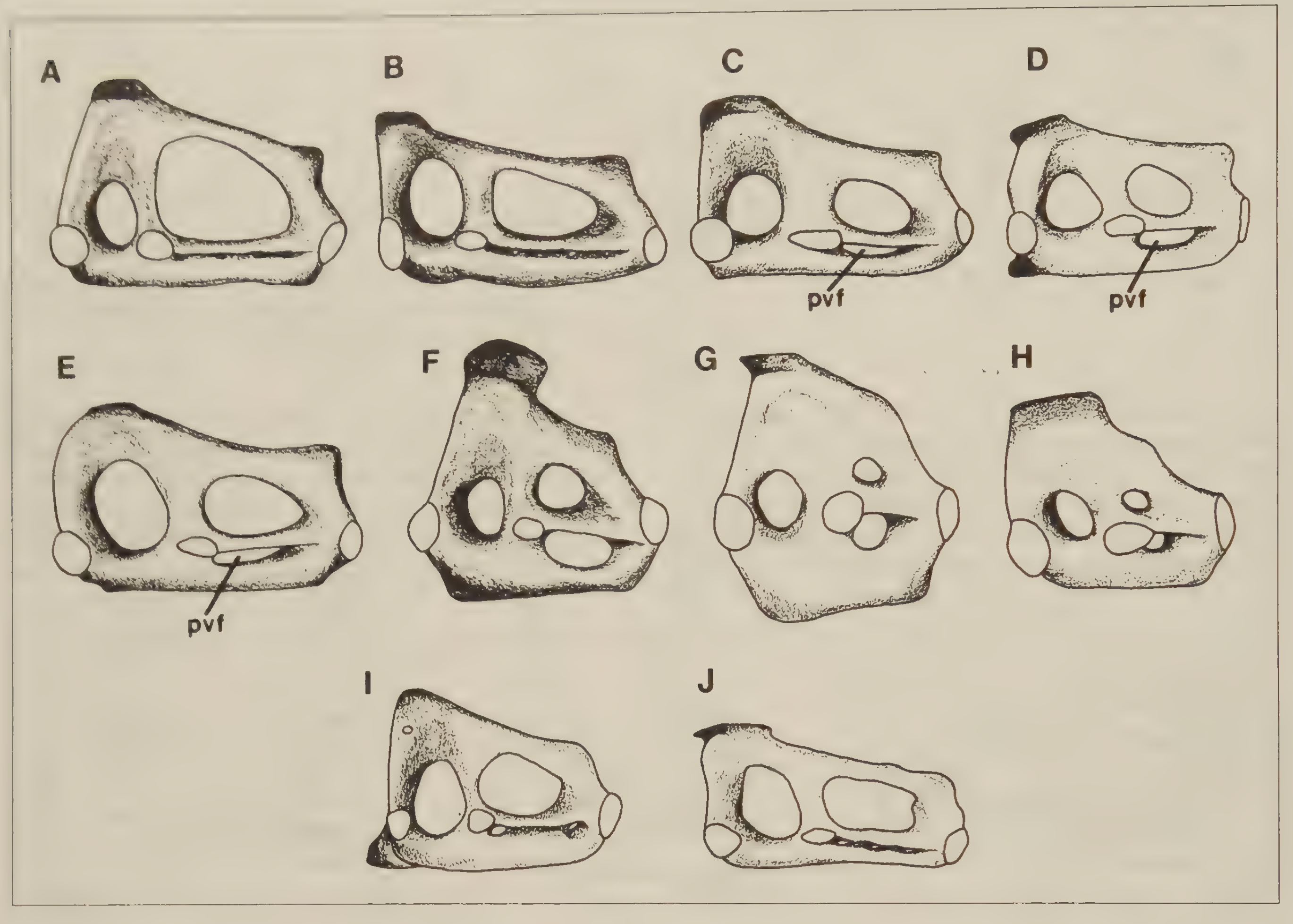


Figure 10.
Lateral view of scapulocoracoids of Group II. A, *Cruriraja rugosa* FM 29861; B, *Anacanthobatis americanus* FM uncat.; C, *Raja* (*Dipturus*) *floridana* USNM uncat.; D, *Raja* (*Okamejei*) *heemstrai* USNM 231866; E, *Raja* (*Raja*) *miraletus* TCWC uncat.; F, *Raja* (*Leucoraja*) *leucosticta* MNHN 1969-208; G, *Breviraja spinosa* FM 298868; H, *Raja* (*Malacoraja*) *senta* TCWC 4179.1; I, *Gurgesiella* (*Fenestraja*) *atripinna* MCZ 41828; J, *Gurgesiella* (*Gurgesiella*) *atlantica* TCWC uncat.

capsules. *Anacanthobatis* also possesses very long lateral prepelvic processes; however, the processes are structurally different from those of *Psammobatis* and *Sympterygia*. *Psammobatis*, with eight species, and *Sympterygia*, with four species, are endemic to temperate South America.

The clade of *Notoraja*, Subgenus A, *Irolita*, *Pseudoraja*, and *Pavoraja* is distinguished by five parallelisms: nasal capsules with basal fenestrae (14); narrow internasal plate (15); expanded and oval-shaped nasal capsules (16); rostral appendices narrow and widely separated from rostral shaft (17); and rostral appendices oval in cross-section (18). The *Malacoraja*, *Fenestraja*, and *Gurgesiella* clade also possesses narrow internasal plates and both expanded and oval-shaped nasal capsules, and the *Fenestraja* and *Gurgesiella* clade also possesses narrow rostral appendices which are widely separated from the rostral shaft and are oval in cross section, and nasal capsules with basal fenestrae. *Notoraja* is the sister group of the other four taxa but is not defined by a derived character state. It comprises two species from the western Pacific and one species from off Madagascar (B. Seret, Mus. Natl. d'Histoire Naturelle, pers. commun., February 1986).

The sister group of *Notoraja* is defined by three parallelisms: absence of an anterior bridge in the scapulocoracoid (1′); clasper glans with the component rhipidion (12) (Fig. 7); and clasper skeleton without a dorsal terminal 1 cartilage (13). Group II also lacks an anterior bridge and possesses a rhipidion. Dorsal terminal 1 cartilages are lacking in *Arhynchobatis* and the *Fenestraja* and *Gurgesiella* clade. Within Group I *Arhynchobatis* also possesses a rhipidion. Subgenus A is the sister group of the three taxon clade, is undefined by derived characters, and consists of two species from New Zealand.

The sister group of Subgenus A is an unresolved trichotomy and is defined by two parallelisms, rostral shaft narrow and of equal width over length (9) and rostral shaft

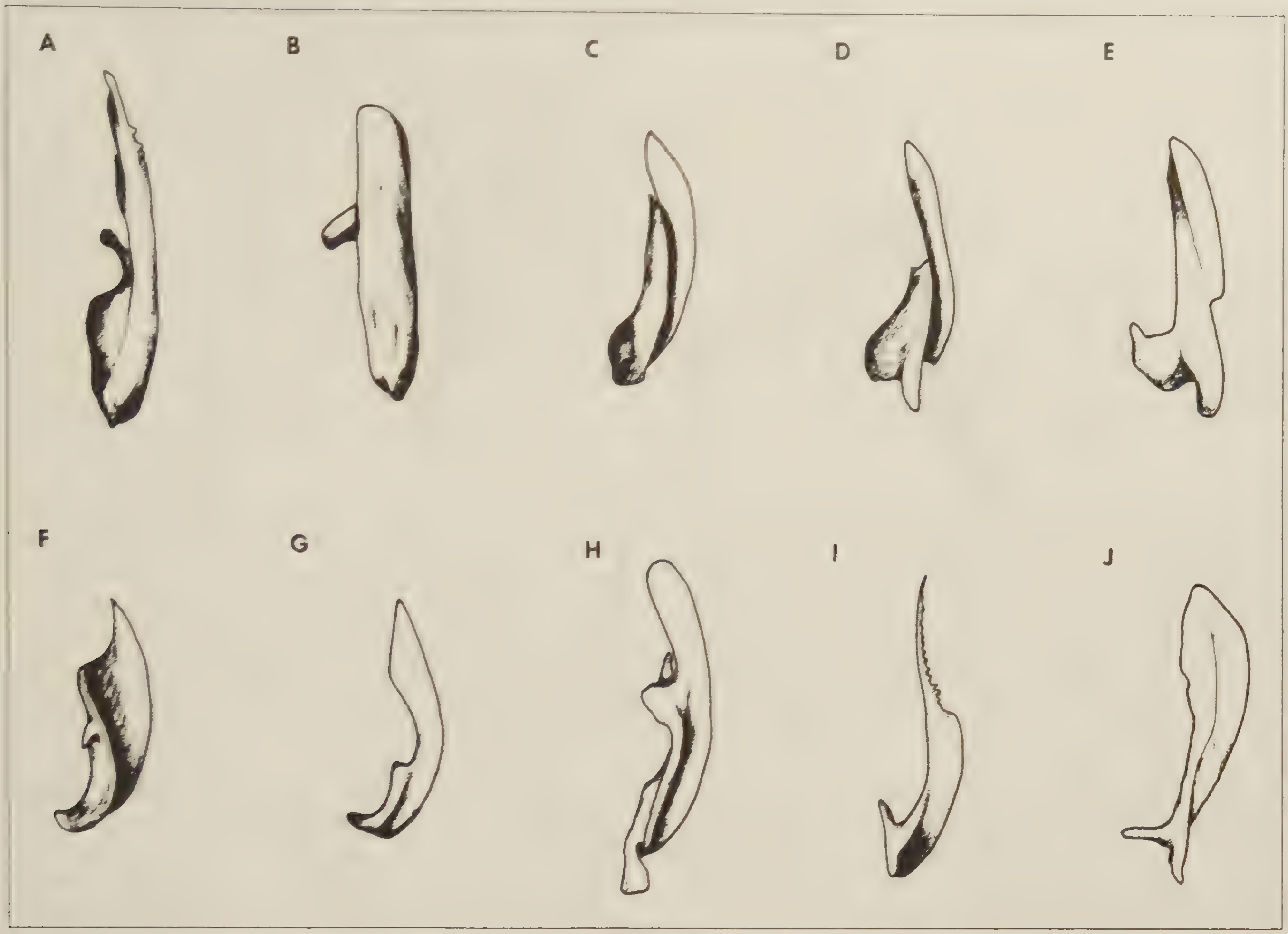


Figure 11.
Ventral terminal cartilages of Group II. A, *Cruriraja poeyi* USNM uncat.; B, *Anacanthobatis longirostris* adapted from Hulley (1973, Fig. 8); C, *Raja (Dipturus) teevani* MCZ 41901; D, *Raja (Okamejei) fusca* MCZ 40326; E, *Raja (Raja) microocellata* TCWC 2819.3; F, *Raja (Leucoraja) erinacea* TCWC uncat.; G, *Breviraja schroederi* MCZ 40232; H, *Raja (Malacoraja) senta* TCWC uncat.; I, *Gurgesiella (Fenestraja) sibogae* ZMA 113.491; J, *Gurgesiella (Gurgesiella) furvescens* TCWC uncat.

segmented at base (11) (Fig. 6). The clade *Bathyraja*, *Arhynchobatis*, and *Psammobatis* also possesses a slender rostral shaft, and *Arhynchobatis* and *Psammobatis* have basally segmented rostral shafts. *Irolita* is a monotypic Australian taxon defined by two reversals: presence of a slender anterior bridge in the scapulocoracoid (1) (Fig. 9) and a broad internasal plate (15), and two parallelisms, anterior fontanelle of neurocranium broad and extending little beyond leading edge of nasal capsules (10) and rostral shaft free of rostral node (19) (Fig. 6). A broad internasal plate is a synplesiomorphic character state of Rajoidei and a slender anterior bridge is a synapomorphy in Group I. Broad anterior fontanelles are present in the *Bathyraja*, *Arhynchobatis*, and *Psammobatis* clade, and rostral shafts free of the rostral node occur in the *Fenestraja* and *Gurgesiella* clade of Group II. *Pseudoraja* is a monotypic taxon endemic to the western North Atlantic and is distinguished by a reversal, scapulocoracoid with a slender anterior bridge (1). The outgroup, Subgenus A, lacks the anterior bridge. *Pavoraja* comprises six Australian species and is defined by one reversal, presence of the dorsal terminal 1 clasper cartilage (13).

Group II is defined by two parallelisms: scapulocoracoids without an anterior bridge (1′) (Fig. 10) and clasper glans with the component rhipidion (12); and two synapomorphies, clasper glans greatly expandable (20) and clasper glans with component shield (21) (Fig. 11) formed by the sharp lateral edge of the ventral terminal cartilage. The greatly expandable glans and the component shield are unique to Group II. The scapulocoracoids of Subgenus A and *Pavoraja* also lack an anterior bridge and a rhipidion is also found in *Arhynchobatis*, *Irolita*, Subgenus A, and *Pavoraja*.

Interrelationships within Group II are not completely resolved (Fig. 1). However, all trees grouped *Cruriraja* and *Anacanthobatis*; *Dipturus*, *Okamejei*, and *Raja*; *Leucoraja* and *Breviraja*; and *Malacoraja*, *Fenestraja*, and *Gurgesiella*.

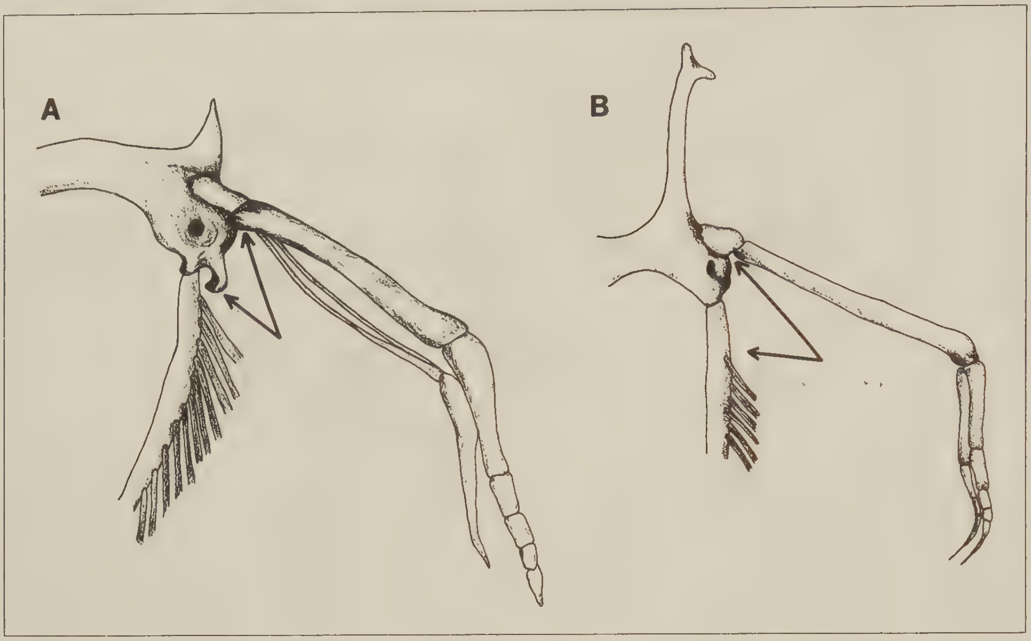


Figure 12.
Pelvic girdles. A, *Cruriraja rugosa* FM 29861; B, *Anacanthobatis americanus* FM uncat. Arrows indicate gap in distribution of radials.

Cruriraja and *Anacanthobatis* share two synapomorphies, pelvic fins externally separated into an anterior and a posterior lobe (22), and proximal section of metapterygium of pelvic girdle without radials (23) (Fig. 12). *Cruriraja* comprises eight species found in the western North Atlantic, eastern South Atlantic, western South Indian Ocean, and central Indian Ocean. Anacanthobatis comprises 7 to 10 species located in the western North Atlantic, western South Indian Ocean, and western North Pacific.

The *Dipturus*, *Okamejei*, and *Raja* clade is defined by three synapomorphies: clasper glans without the component eperon formed by the anterolateral margin of the ventral terminal cartilage (24) (Fig. 11); ventral terminal and accessory terminal 1 cartilages connected by thick connective tissue sheath or by accessory terminal 3 cartilage (25) (Fig. 13); and scapulocoracoids with an expanded postventral fenestra (26) (Fig. 10). All three of the other clades of Group II possess the component eperon and none of the other clades, nor Group I, possesses a similar connection between the ventral terminal and accessory terminal cartilages or an expanded postventral fenestra.

Dipturus is the sister group of *Okamejei* and *Raja* and consists of about 28 species but is presently undefined by a derived character state. All three taxa are subgenera of *Raja*. *Raja* (*Okamejei*) and *R.* (*Raja*) share one synapomorphy, accessory terminal 1 cartilage with an expanded and disc-shaped or blade-shaped tip (27) (Fig. 14). This character state is unique to these two taxa and to three other supraspecific taxa combined with them in the analysis: *R.* (*Rostroraja*), a monotypic taxon from the eastern Atlantic and southeastern Indian Ocean, a North Pacific assemblage of six species of *Raja*, and an amphi-American assemblage of seven species of *Raja* (McEachran and Miyake 1986). The relationships of these five supraspecific

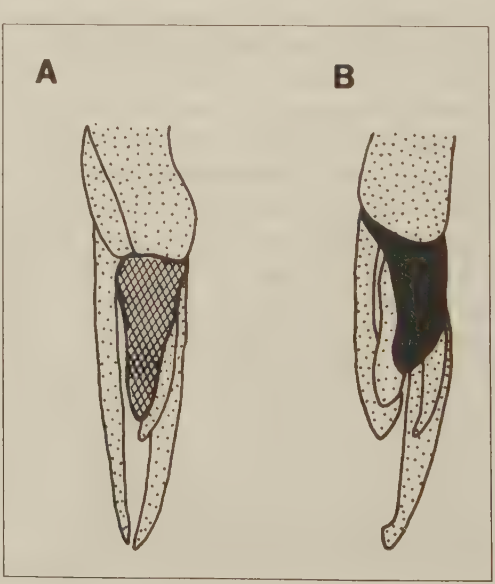


Figure 13.
Ventral view of clasper skeleton with ventral terminal cartilage removed. A, *Raja* (*Dipturus*) *teevani* MCZ 41901; B, *Raja* (*Raja*) *miraletus* TCWC uncat. Stippled area represents fibrous connective tissue joining accessory terminal 1 cartilage and ventral terminal cartilage. Solid area represents accessory terminal 3 cartilage joining accessory terminal 1 cartilage and ventral terminal cartilage.

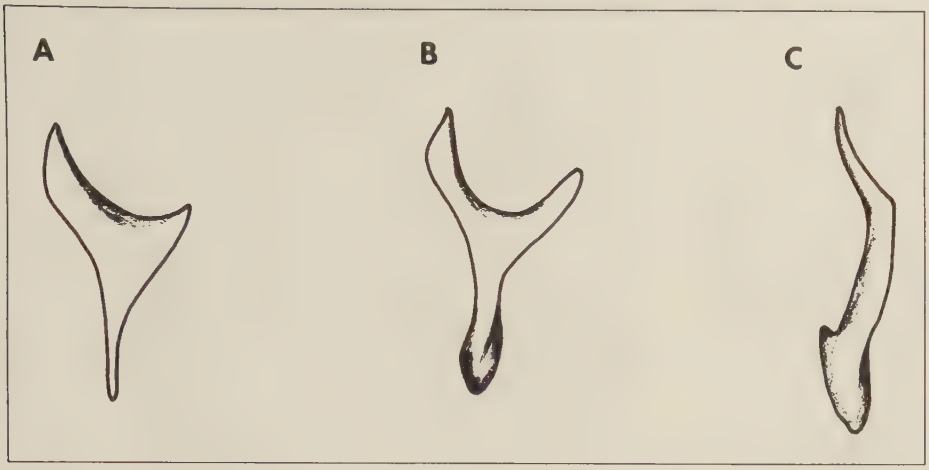


Figure 14.
Dorsal view of accessory terminal 1 clasper cartilage. A, *Raja* (*Dipturus*) *teevani* MCZ 41901; B, *Raja* (*Okamejei*) *fusca* MCZ 40326; C, *Raja* (*Raja*) *microocellata* TCWC 2819.3.

taxa have not been fully elucidated (McEachran and Miyake 1986).

The *Leucoraja* and *Breviraja* clade is defined by one reversal, scapulocoracoid with a postdorsal foramen rather than an expanded fenestra (2) (Fig. 10), and three synapomorphies, rostral appendices flattened, triangular shaped and distinctly separated from the rostral shaft (29) (Fig. 15), dorsal marginal cartilage of clasper skeleton without a distal extension entering the clasper glans (30) and ventral terminal cartilage of clasper skeleton expanded proximally (31) (Fig. 11). These character states are thought to be unique to these taxa and to *Amblyraja* (9 species), *Dactylobatus* (2 species) and *Rajella* (14 species), which are combined with them in the analysis. *Leucoraja*, *Amblyraja*, and *Rajella* are considered to be subgenera of *Raja*. *Raja* (*Leucoraja*) comprises 10 species and is distributed in the Atlantic and eastern South Indian Ocean. *Breviraja* (six species) and *Dactylobatus* are limited to the western North Atlantic. *Raja* (*Amblyraja*) is distributed in the Atlantic, North Pacific, and Indian oceans. *Raja* (*Rajella*) is found in the Atlantic, eastern South Pacific, and Indian oceans. The interrelationships within these five taxa have not been elucidated.

The *Malacoraja*, *Fenestraja*, and *Gurgesiella* clade is defined by two synapomorphies: preorbital processes of neurocranium degenerate (32) (Fig. 15) and ventral terminal cartilage of clasper skeleton, check-shaped with distal process forming component funnel and distomedial process meeting axial cartilage (33) (Fig. 11) and two parallelisms, internasal plate of neurocranium narrow (15) (Fig. 16) and nasal capsules expanded and oval-shaped (16) (Fig. 15). The three other clades of Group II (Figs. 15, 17) and Group I (Figs. 5, 6) possess moderately to well developed preorbital processes and the ventral terminal cartilages of *Malacoraja*, *Fenestraja*, and *Gurgesiella* is unique within Rajoidei. A narrow internasal plate and expanded and oval-shaped nasal capsules also occur in the *Notoraja*, Subgenus A, *Irolita*, *Pseudoraja*, and *Pavoraja* clade.

Malacoraja consists of three species from the Atlantic but is currently undefined by derived characters. The sister group of *Malacoraja*, *Gurgesiella* (*Fenestraja*), and *G.* (*Gurgesiella*) is defined by one synapomorphy, nasal capsules bulging into the precerebral space (34) (Fig. 15) and six parallelisms: propterygia of pectoral girdle reaching rostral node (7); dorsal terminal 1 clasper cartilage absent (13); nasal capsules with basal fenestrae (14); rostral appendices non-plate-like and widely separated from the rostral shaft (17); posterior extensions of rostral appendices conical in cross-section (18); and rostral shaft free of rostral node (19). The nasal capsules of *Pseudoraja* also bulge into the precerebral space (Fig. 6) (McEachran and Compagno 1979), but the fact that nasal capsules and anterior fontanelles are structurally different in these two clades suggests that the character state was acquired separately. The parallelisms occur in various clades of Group I. *Neoraja*, which consists of four species endemic to the Atlantic, was combined with *Gurgesiella* in the analysis. *Neoraja* shares several synapomorphies with *Malacoraja* in addition to sharing parallelisms 7, 17, 18 and 19 with *Gurgesiella*, and is regarded as the sister group of *Gurgesiella* (McEachran and Compagno 1982). *Gurgesiella* (*Fenestraja*) consists of seven species which are endemic either to the western Atlantic or to the Indian Ocean. *Gurgesiella* (*Gurgesiella*) consists of three species which are endemic to the eastern South Pacific, to the western North Atlantic, or to the western South Atlantic.

Discussion

The phylogenetic analysis partially resolved the interrelationships within Rajoidei, revealed several taxonomic areas in which further research is needed to elucidate the interrelationships, suggested wide-scale character state parallelisms and reversals, and partially refuted an empirically derived phylogenetic hypothesis of the taxon (McEachran 1984). The interrelationships within Group I were resolved except for the clade *Irolita*, *Pseudoraja*, and *Pavoraja* and for the status of *Bathyraja* and *Rhinoraja*. Also the clade of

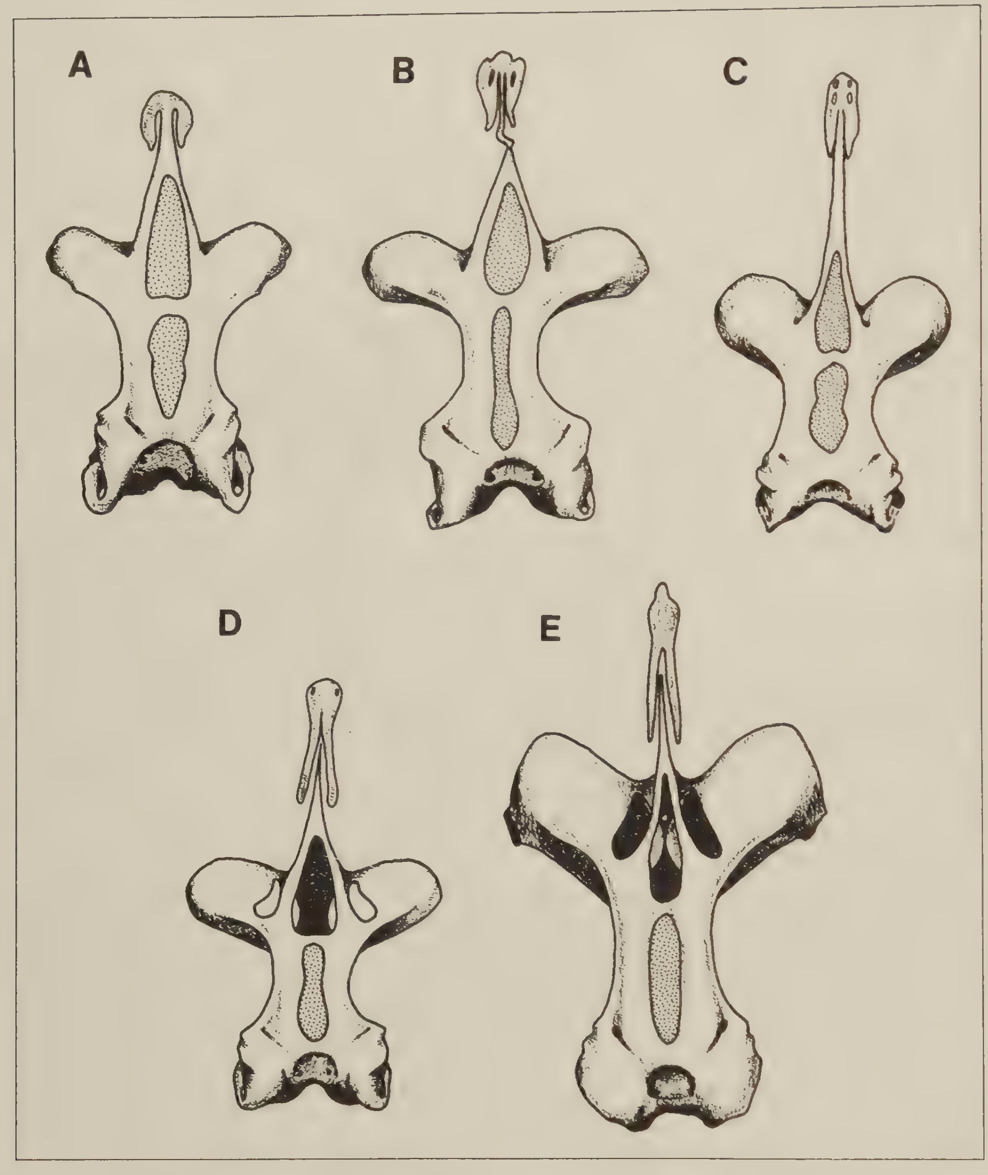


Figure 15.
Dorsal view of neurocrania. A, *Raja* (*Leucoraja*) *ocellata* TCWC uncat.; B, *Breviraja colesi* MCZ 41998; C, *Raja* (*Malacoraja*) *senta* TCWC uncat.; D, *Gurgesiella* (*Fenestraja*) *sibogae* ZMA 112.640; E, *Gurgesiella* (*Gurgesiella*) *furvescens* TCWC uncat.

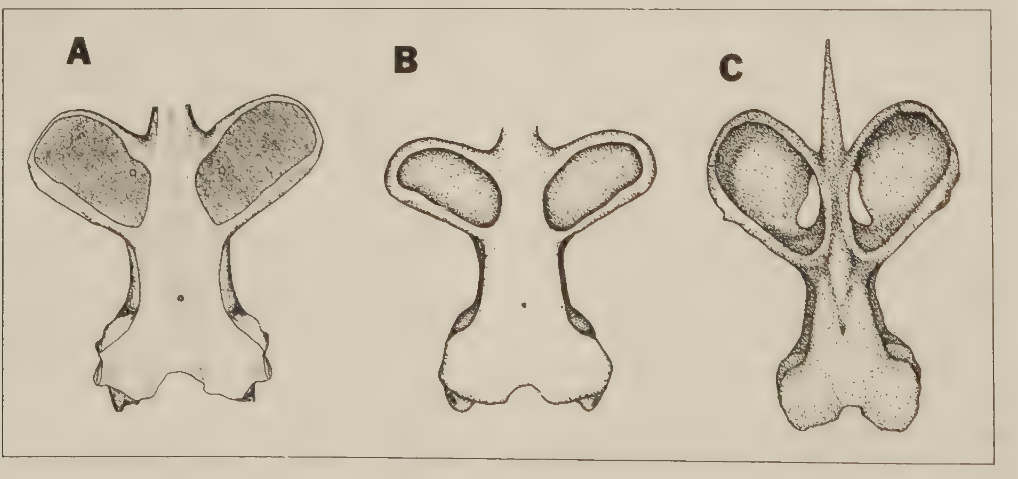


Figure 16.
Ventral view of neurocrania. A, *Raja* (*Malacoraja*) *senta* TCWC uncat.; B, *Gurgesiella* (*Fenestraja*) *sibogae* 112,640; C, *Gurgesiella* (*Gurgesiella*) *atlantica* TCWC uncat.

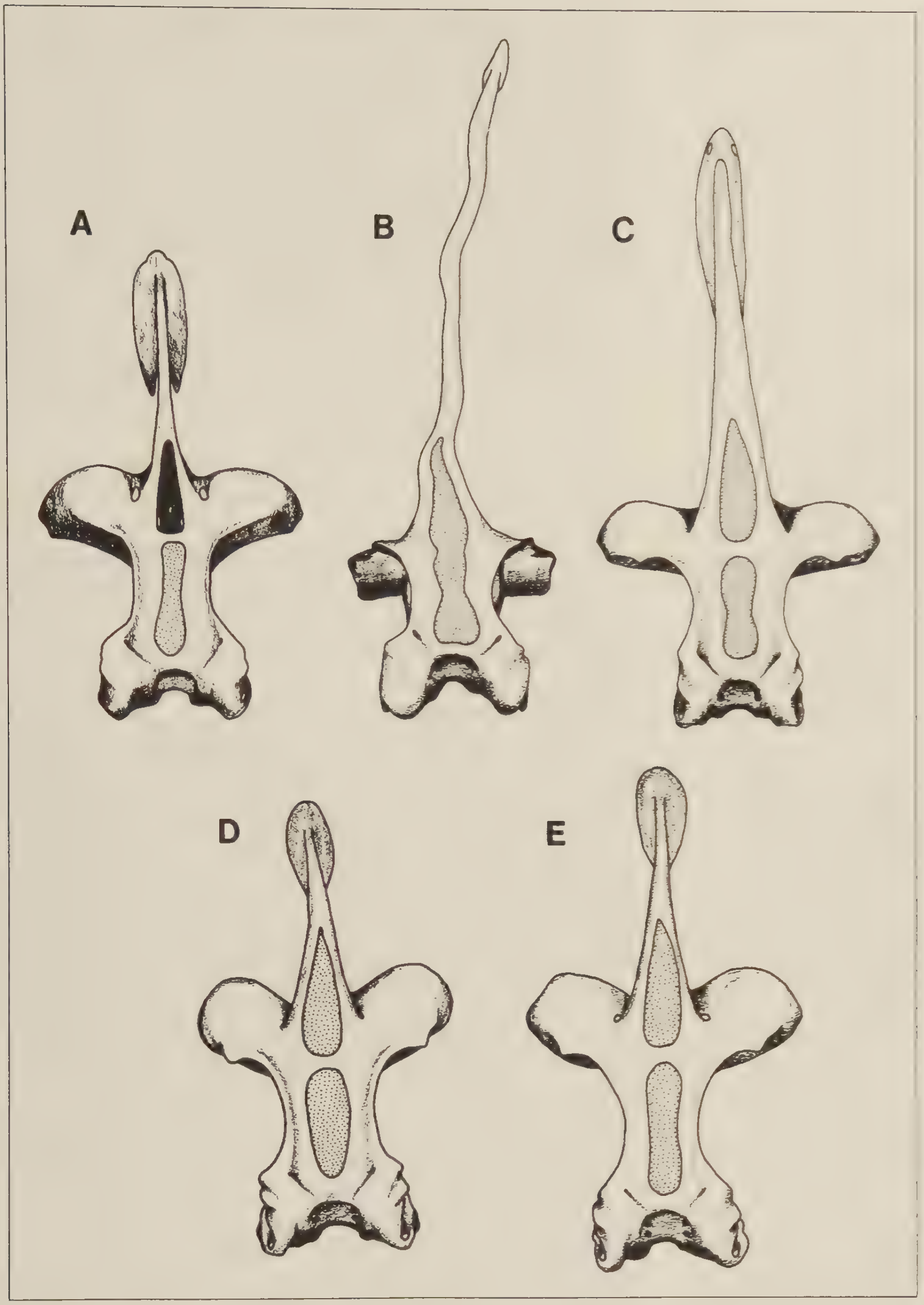


Figure 17.
Dorsal view of neurocrania. A, *Cruriraja rugosa* FM 29861; B, *Anacanthobatis americanus* FM uncat.; C, *Raja* (*Dipturus*) *johannisdavisi* BMNH 1939.5.24.19; D, *Raja* (*Okamejei*) *schmidti* MCZ 40325; E, *Raja* (*Raja*) *miraletus* TCWC uncat.

Bathyraja, *Arhynchobatis*, and *Psammobatis* was united by homoplasies rather than synapomorphies. *Irolita* and *Pseudoraja* share a putative synapomorphy which was not included in the analysis, proximal tip of rostral shaft separated from rostral base. It was decided to exclude this synapomorphy and treat the three taxa as a trichotomy pending the availability of a clasper of *Pseudoraja*. Presently there are no mature male specimens of *Pseudoraja* available for study.

No derived character states were discovered that define either *Bathyraja* or *Rhinoraja* and thus one or both of these taxa may be paraphyletic. However, neither of these putative taxa have been studied in great detail. Research by Ishiyama (1958, 1967), Stehmann (1970), Hulley (1972a), Ishiyama and Ishihara (1977), and Ishihara and Ishiyama (1985, 1986) suggests that the clasper structure of these taxa is relatively conservative. Thus elucidation of their interrelationships may depend largely on other character complexes, i.e., neurocrania, scapulocoracoids, ventral gill arch skeletons, and cranial and ventral gill musculature.

Interrelationships within Group II were resolved into four subgroups. Relationships within each of the subgroups was rather highly corroborated but interrelationships among them was not resolved. *Cruriraja* and *Anacanthobatis* share unique specializations of the pelvic girdle. This specialization strongly argues against Hulley's (1973) proposal of placing these taxa in their own families, Crurirajidae and Anacanthobatidae respectively, or his later proposal (Hulley 1986) of placing them in separate families, Rajidae and Anacanthobatidae.

Raja (*Dipturus*), *R.* (*Okamejei*), and *R.* (*Raja*), plus the taxa combined with them in the analysis, *R.* (*Rostroraja*), a north Pacific *Raja* assemblage and a amphi-American *Raja* assemblage, share three synapomorphies strongly suggesting that they form a monophyletic group. *Raja* (*Dipturus*) is considered to be the sister group of the rest of the clade. Presently it is undefined by derived characters, possibly because it includes species which are members of one of the four derived taxa. A number of the species of *R.* (*Dipturus*) and of the other taxa remain to be studied before the interrelationships within this subgroup are more fully resolved.

Raja (*Leucoraja*) and *Breviraja*, plus the taxa combined with them in the analysis, *R.* (*Amblyraja*), *R.* (*Rajella*), and *Dactylobatus*, share three synapomorphies suggesting that they form a monophyletic subgroup. Interrelationships within this subgroup have not been investigated in great detail.

Raja (*Malacoraja*), *Gurgesiella* (*Fenestraja*), and *G.* (*Gurgesiella*), plus the taxon combined with them in the analysis, *Neoraja*, share two unique character states which suggest that they form a monophyletic subgroup. *Raja* (*Malacoraja*) is considered the sister group of the remainder of the clade. It was thought to possess a synapomorphy, denticles distributed along the ventral surface of the tail (McEachran 1984). However, this character state is also found in some species of *R.* (*Rajella*). *Neoraja* shares several derived character states or parallelisms with *R.* (*Malacoraja*) and others with *Gurgesiella* but is considered the sister group of *Gurgesiella* (McEachran and Compagno 1982).

Interrelationships among the four subgroups of Group II may be further elucidated once more of the species have been examined in detail. This, however, may require the incorporation of additional characters, less variable than those thus far used. The ventral gill arch skeleton varies between Group I and Group II, and detailed study of this character complex may aid in further refining the interrelationships within Group II. Miyake (1988) discovered differences in the cephalic and branchial gill arch musculature in several taxa of Group II and a comprehensive survey of this character complex may be fruitful.

The relatively low consistency index of the most parsimonious trees and the relatively low value for Mickevich's (1978) consensus index of the strict consensus tree are due to the high number of homoplasies in the character matrix. There are a total of 36 parallelisms and reversals in the most parsimonious trees. The homoplasies suggest widescale mosaic evolution and distinct evolutionary trends within Rajoidei. Many of the more derived taxa of both Group I and Group II possess very slender rostral shafts which are separate from either the rostral base (Group I) or the rostral node (Group I): laterally expanded nasal capsules with a basal fenestra; neurocrania with slender basal and internasal plates; neurocrania with either slender jugal arches or lacking jugal arches; anteroposteriorly expanded scapulocoracoids, with an expanded postdorsal fenestra; propterygia of the pectoral girdle which extend to the rostral node; and structurally simple claspers which lack the dorsal terminal 1 cartilage. In addition to the parallel development of these character states in Group I and Group II, many of these character states have apparently been independently acquired within several taxonomic assemblages of Group II. One species of *Anacanthobatis*, *A. marmoratus*, and *Gurgesiella* apparently have independently acquired basal fenestra on the nasal capsules (Seret 1986b). *Breviraja*, *G.* (*Fenestraja*), and *G.* (*Gurgesiella*) have apparently separately developed very slender rostral shafts. *Gurgesiella* (*Fenestraja*) and *G.* (*Gurgesiella*); *Cruriraja* and *Anacanthobatis*; and *Dipturus*, *Okamejei*, and *Raja* have separately evolved elongated scapulocoracoids with expanded postdorsal fenestra.

The high frequency of homoplasies and an inadequate anatomical survey led to a misinterpretation of the interrelationships in McEachran's (1984) phylogenetic hypothesis. In this study it was assumed that absence of the anterior bridge of the scapulocoracoid and presence of a rhipidion were synapomorphies of Group II. Lateral horns on the basihyal and a spoon-shaped ventral terminal cartilage were not recognized as synapomorphies in Group I. McEachran (1984), based on Ishiyama (1958, 1967), assumed that Subgenus A was very similar to or synonymous with *Notoraja* and for that reason refrained from formally recognizing it. A subsequent examination of *Notoraja tobitukai*, the only described species of the taxon, and Stehmann's (in press) description of a new species of *Notoraja* revealed that *Notoraja* differs from Subgenus A by lacking an anterior bridge in the scapulocoracoid. This suggested that the anterior bridge has been lost twice within Rajoidei, once in Group I and once in Group II. Reinterpretation of the scapulocoracoid transition led to a reevaluation of some of the other anatomical characters and resulted in the current phylogenetic hypothesis.

Because the phylogenetic interrelationships proposed in this study are considered a working hypothesis, no taxonomic changes are recommended at this time. Group I and Group II are considered family level taxa. Group II includes the type species of Rajidae, *R. miraletus* Linneaus. Thus Group II is equivalent to Rajidae. Group I includes the type species of Arhynchobatidae, *Arhynchobatis asperrimus* Waite. Arhynchobatidae is the oldest familial level taxon of Group II, but we will refrain from naming this taxon until the interrelationships within it are more highly corroborated.

As presently constituted, the genus *Raja* is polyphyletic. It is applied to species in Group I and to species in three of the four subgroups in Group II. This problem can be easily solved by elevating the subgenera of *Raja* to genera. However, we recommend against such a move until the interrelationships of the supraspecific taxa have been more fully resolved.

McEachran (1984) removed two species from *Bathyraja* (*B. asperula* and *B. spinifera*) and classified them as an unnamed subgenus (Subgenus A) in the genus *Pavoraja*. However, in the present study Subgenus A was classified as the sister group of the *Irolita*, *Pseudoraja*, *Pavoraja* clade. We recommend no further nomenclature designations until the relationships among these supraspecific taxa have been further elucidated.

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Zoogeography and Bathymetry of Skates (Chondrichthyes, Rajoidei)

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ABSTRACT

The zoogeography and bathymetry of skates was studied from a phylogenetic perspective. The phylogenetic data base was a strict consensus tree of phylogenetic analysis using the parsimony (PAUP) program. Distributional data and bathymetric data of all 224 to 227 species of skates were obtained from the literature and from museum records. The two familial level taxa of skates (Group I and Group II) broadly overlap but have different centers of abundance. Group I occurs almost exclusively in the Pacific and in the western South Atlantic, while Group II occurs predominately in the North Atlantic, eastern South Atlantic-western Indian Ocean, and the western Pacific. Within Group I the *Raja* (*Atlantoraja*)–*R.* (*Rioraja*) clade is limited to the warm temperate western South Atlantic, while its sister group, Subgroup Ia and Subgroup Ib, ranges throughout the Pacific, the southern Indian Ocean, and the western South Atlantic. Subgroup Ia is largely antitropical in the Pacific and is warm temperate to polar in the southern Hemisphere. Subgroup Ib has a tropical to warm temperate distributional track extending from the southwestern Indian Ocean to the western Pacific and western North Atlantic. Within Group II *Gurgesiella* (*Fenestraja*) has a distributional track extending from the tropical western North Atlantic to the northeastern Indian Ocean and western North Pacific. *Raja* (*Dipturus*) has a circum-tropical-temperate distributional track, except it is absent in the tropical western Pacific and most of the eastern Pacific. Subgroup IIc and *Malacoraja* and *Neoraja* of Subgroup IId are largely restricted to the Atlantic. *Raja* (*Amblyraja*), *R.* (*Rajella*), *Malacoraja*, and *Neoraja*, and to a lesser extent *R.* (*Leucoraja*), display an antitropical distribution, while *Breviraja* and *Dactylobatus* are limited to the tropical to temperate western North Atlantic.

Introduction

Skates are unique among chondrichthyans in their species diversity, their ubiquity within the marine environment, and in the restrictedness of individual species ranges. Also supraspecific taxa (subgenera and genera) often appear to have unique zoogeographical patterns, and supraspecific sister taxa and sister species often appear to have vicariant (parapatric or allopatric) distributional patterns. These properties and the fact that skates are relatively well known systematically suggest that a zoogeographic study of skates is in order and that it would be of general interest to researchers investigating zoogeographic patterns of marine benthic organisms.

There are about 224 to 227 species of skates, in about 29 supraspecific taxa and two familial level taxa (Appendix; McEachran and Miyake 1990). About one half of these species were described within the last 40 years, and an additional 20 or more species in collections around the world remain to be described.

Skates are entirely marine in habitat and within this habitat they are nearly ubiquitous along continental and insular margins, with the exception of the Pacific Plate (Springer 1982), the Red Sea (Fowler 1956; Gohar and Mazhar 1964), the Persian Gulf, and at depths below 3000 m (Grey 1956). At temperate latitudes they occur from the sublittoral zone to abyssal depths but at tropical and polar latitudes they are restricted to the outer half of the continental shelf to abyssal depths. They are rare or absent over hard or calcarious bottoms.

Unlike the majority of chondrichthyans, many skates have rather small distributional ranges. At least one species is endemic to the Gulf of California (McEachran and Miyake 1988). Sixteen of the 41 species of skates occurring from Cape Hatteras, North Carolina to the mouth of the Amazon in the western North Atlantic are endemic to one of the zoogeographical subareas of this region, i.e., southeastern United States (Cape Hatteras to the Dry Tortugas, Florida); Gulf of Mexico, Caribbean (Cape Catoche, Yucatan to the Equator); or the West Indies (Greater and Lesser Antilles, and Bahamas) (McEachran and Branstetter. unpubl. data). Five of the 17 species occurring in the Mediterranean and off the northern coast of Morocco are endemic to this region (Stehmann and Bürkel 1984), 13 of the 22 species occurring off South Africa are endemic (Hulley 1972), two of the three species reported from Kerguelen and Heard islands in the southern Indian Ocean are endemic (Stehmann 1985), three of the four species of *Rhinoraja* are endemic to northern Japan (Ishiyama 1958), and the other species of *Rhinoraja* is endemic to Kamchatka Peninsula (Dolganov 1985). Similar patterns probably occur in other areas, but collections are inadequate for defining species ranges.

Cladistic analyses of a number of supraspecific taxa of skates suggest that many sister species and supraspecific sister taxa have vicariant distributional patterns. Sister species or subspecies often have allopatric distributions separated by recent geological formations, i.e., Isthmus of Panama (McEachran and Compagno 1979) and Florida Peninsula (McEachran 1977), or by steep thermal gradients (McEachran 1977; McEachran et al. 1989). Other sister species display parapatric distributional patterns (McEachran and Matheson 1985; McEachran and Miyake 1987), or partially sympatric distributions (McEachran 1982, 1983). Supraspecific sister taxa also display allopatric or parapatric distributions (McEachran and Miyake 1986).

There have been a number of regional zoogeographical studies of skates (Ishiyama 1958; Stehmann 1970, 1976; Hulley 1972; Menni 1972, 1973; Menni and Gosztonyi 1982; Menni and Lopez 1984) and zoogeographical studies of supraspecific taxa (Hulley 1973; Seret 1986; Stehmann 1986) but no comprehensive worldwide studies treating the entire suborder. Ishiyama (1958) briefly dealt with the zoogeography of the 21 species of skates found in Japanese waters. He classified them in the genera *Breviraja* (= *Bathyraja*), *Rhinoraja*, and *Raja* (within subgenera *Tengujei* (= *Dipturus*) and *Okamejei*). *Bathyraja* occurred from the northern waters of Japan to the Sea of Okhotsk, or in the case of two species, to the eastern North Pacific. *Rhinoraja*, with three species, was endemic to the waters of northern Japan. *Raja* was distributed from southern Japan to the South China Sea. The distribution of the northern forms, *Bathyraja* and *Rhinoraja*, and the southern form, *Raja*, overlapped off northern and central Japan. Ishiyama considered the skate fauna of the western North Pacific to be more similar to that of the eastern North Pacific than to other areas of the Pacific because several of the northern Japanese species also occurred in the eastern North Pacific. He also considered the skate faunas of the North Pacific and North Atlantic to be similar because they shared two genera, *Breviraja* (= *Bathyraja*) and *Raja*. *Breviraja* was later divided into two genera, *Breviraja* from the western North Atlantic and *Bathyraja* from the North Pacific (Ishiyama and Hubbs 1968). Ishiyama reasoned that the North Pacific fauna originated in the North Atlantic because of the greater generic and specific diversity of skates in the Atlantic.

Stehmann (1970) revised the skates of the eastern North Atlantic. He classified the 22 species from this region in two genera, *Bathyraja* and *Raja*, and six subgenera, *R.* (*Amblyraja*), *R.* (*Dipturus*), *R.* (*Leucoraja*), *R.* (*Malcoraja*), *R.* (*Raja*), and *R.* (*Rajella*). He stated that *Bathyraja* was antitropical in all oceans and had a center of abundance in the northwestern Pacific. *Raja* (*Amblyraja*) was bipolar with species in the North Atlantic, South Atlantic, Antarctic, and eastern Pacific. *Raja* (*Dipturus*) was found worldwide from the outer continental shelf to archibenthal depths. *Raja* (*Leucoraja*) and *R.* (*Raja*) were thought to be limited to the eastern Atlantic where they occurred from the continental shelf to archibenthal depths. Unlike *R.* (*Leucoraja*), *R.* (*Raja*) was widely distributed in the eastern South Atlantic. *Malacoraja* and *R.* (*Rajella*) were found on both sides of the North Atlantic at archibenthic depths. Stehmann (1970) estimated that 11 of the 22 species that he studied were endemic to the eastern North Atlantic.

Hulley (1972, 1973) revised the skates of South African waters. He classified the 24 species from this region in *Anacanthobatis*, *Bathyraja*, *Cruriraja*, and *Raja*. He classified the species of *Raja* in the six subgenera erected by Stehmann plus an additional one, *R.* (*Rostroraja*), representing a single species ranging from the eastern North Atlantic to South Africa. He estimated that 13 of these species were endemic to South Africa and that the remaining extended from the eastern North Atlantic or the tropical eastern Atlantic to South Africa. The skate fauna of South Africa was most similar to that of the eastern North Atlantic, although South Africa shared three genera, *Anacanthobatis*, *Breviraja*, and *Cruriraja*, exclusively with the western North Atlantic.

Menni (1972, 1973) revised the skate fauna of the western South Atlantic, from southern Brazil to northern Argentina. He classified the 13 species in three genera, *Bathyraja*, *Raja*, and *Sympterygia*, and four subgenera, *R.* (*Amblyraja*), *R.* (*Atlantoraja*), *R.* (*Dipturus*), and *R.* (*Rioraja*). He noted that only four of these taxa occurred in the eastern South Atlantic and that the skate fauna of the western South Atlantic was distinct from that of the remainder of the Atlantic. Menni and Gosztonyi (1982) and Menni and Lopez (1984) described the distributional patterns of skates that occur off the Argentine coast.

Stehmann (1976) revised the skate fauna of the northern Indian Ocean and placed the eight nominal species of this region in seven previously recognized taxa, *Breviraja*, *Cruriraja*, *Raja* (*Amblyraja*), *R.* (*Dipturus*), *R.* (*Okamejei*), *R.* (*Rajella*), and *R.* (*Rostroraja*). He stated that for topographical and climatic reasons the northern Indian Ocean was not a center of radiation of skates, and that the skates that

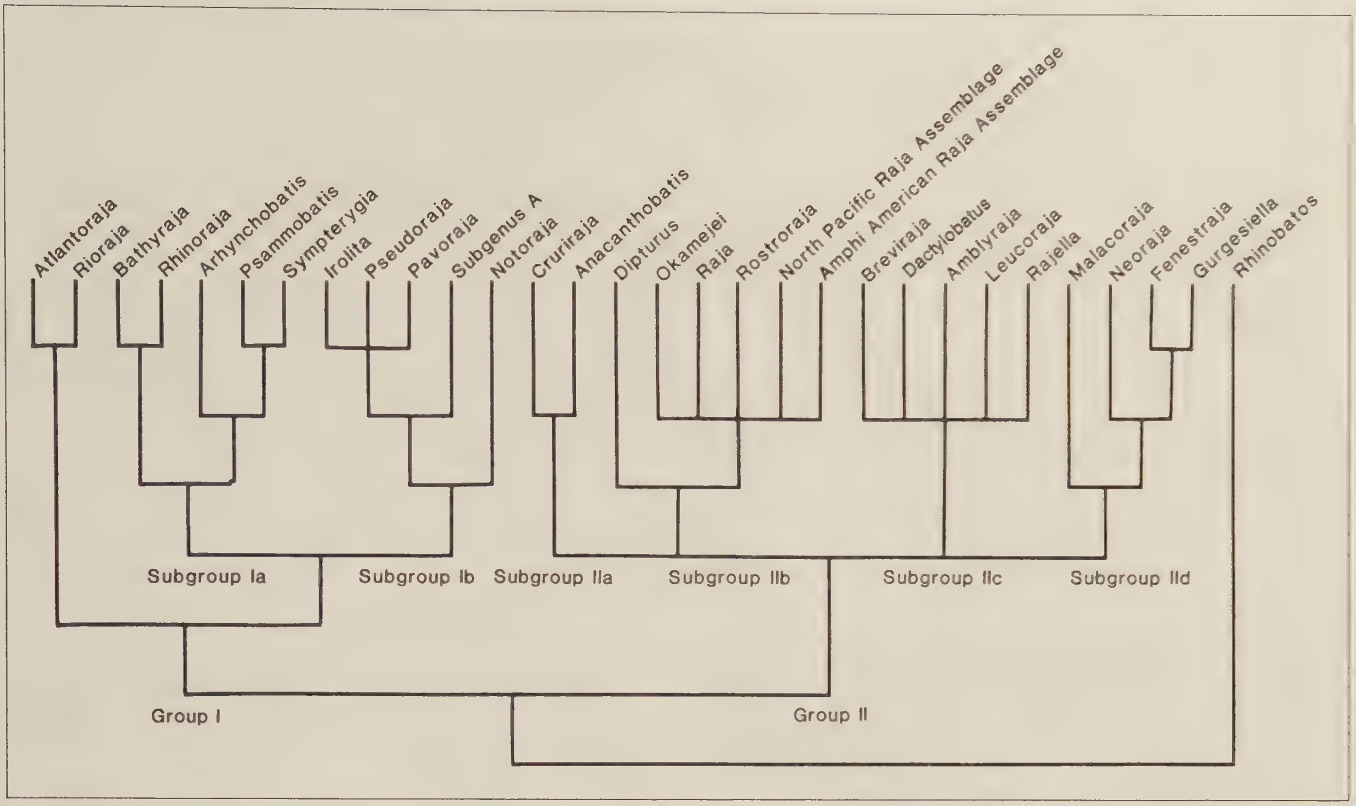
Atlantoraja
Rioraja
Bathyraja
Rhinoraja
Arhynchobatis
Psammobatis
Sympterygia
Irolita
Pseudoraja
Pavoraja
Subgenus A
Notoraja
Cruriraja
Anacanthobatis
Dipturus
Okamejei
Raja
Rostroraja
North Pacific Raja Assemblage
Amphi American Raja Assemblage
Breviraja
Dactylobatus
Amblyraja
Leucoraja
Rajella
Malacoraja
Neoraja
Fenestraja
Gurgesiella
Rhinobatos
Subgroup Ia
Subgroup Ib
Subgroup IIa
Subgroup IIb
Subgroup IIc
Subgroup IId
Group I
Group II

Figure 1.
Strict consensus tree of Rajoidei expanded to include all supraspecific taxa.

occur there migrated from centers of radiation in the Atlantic and western Pacific oceans.

McEachran and Compagno (1982) and McEachran (1984) revised the skate genus *Breviraja*, and split *Breviraja* into three genera, *Breviraja*, *Neoraja*, and *Gurgesiella* (*Fenestraja*). *Breviraja* was restricted to two species from the tropical and warm temperate western North Atlantic. *Neoraja* was erected for two species from the eastern Atlantic, and *Gurgesiella* (*Fenestraja*) was erected for seven species from the tropical and warm temperate Atlantic and northern Indian Ocean. Subsequently, four more species of *Breviraja* were described from the western North Atlantic (McEachran and Matheson 1985; McEachran and Miyake 1987), and two more species of *Neoraja* were described, one from the tropical eastern Atlantic (Stehmann and Seret 1983) and one from the warm temperate western North Atlantic (McEachran and Stehmann 1984).

Stehmann and Bürkel (1984) described the distribution and depth ranges of 31 species of skates that occur in the eastern North Atlantic.

Seret (1986) stated that *Anacanthobatis* occurs in three widely separated areas, the western central Atlantic, the southwestern Indian Ocean, and the China Sea. He suggested that the southwestern Indian Ocean and the China Sea species might share a more recent common ancestry than either does with the western central Atlantic species, or that the southwestern Indian Ocean may have served as a local center of radiation or as a migratory route between the central western Atlantic and the China Sea.

Stehmann (1986) discussed the systematics and distribution of the skate genus *Bathyraja*. He recognized 38 nominal species in three morphotypes and distributional groups that are variously restricted to shallow water, deep water, or water of intermediate depths. The greatest diversity of species occurred in the North Pacific, the western South Atlantic, and Antarctic waters. Each of these areas of high diversity, in Stehmann's opinion, has served as a center of radiation of *Bathyraja*.

The purpose of our study is to examine the geographic and bathymetric distribution of supraspecific taxa of skates from a phylogenetic perspective. The goal of the study is to test the hypothesis that the distribution of supraspecific taxa in space can be explained by their phylogenetic history and by the geological history of their habitats.

Methods

The phylogenetic data base of this study is that of McEachran and Miyake (1990) and is based on phylogenetic analysis using parsimony (PAUP, version 2.40) (Swofford 1986). Data for the analysis consisted of 19 supraspecific

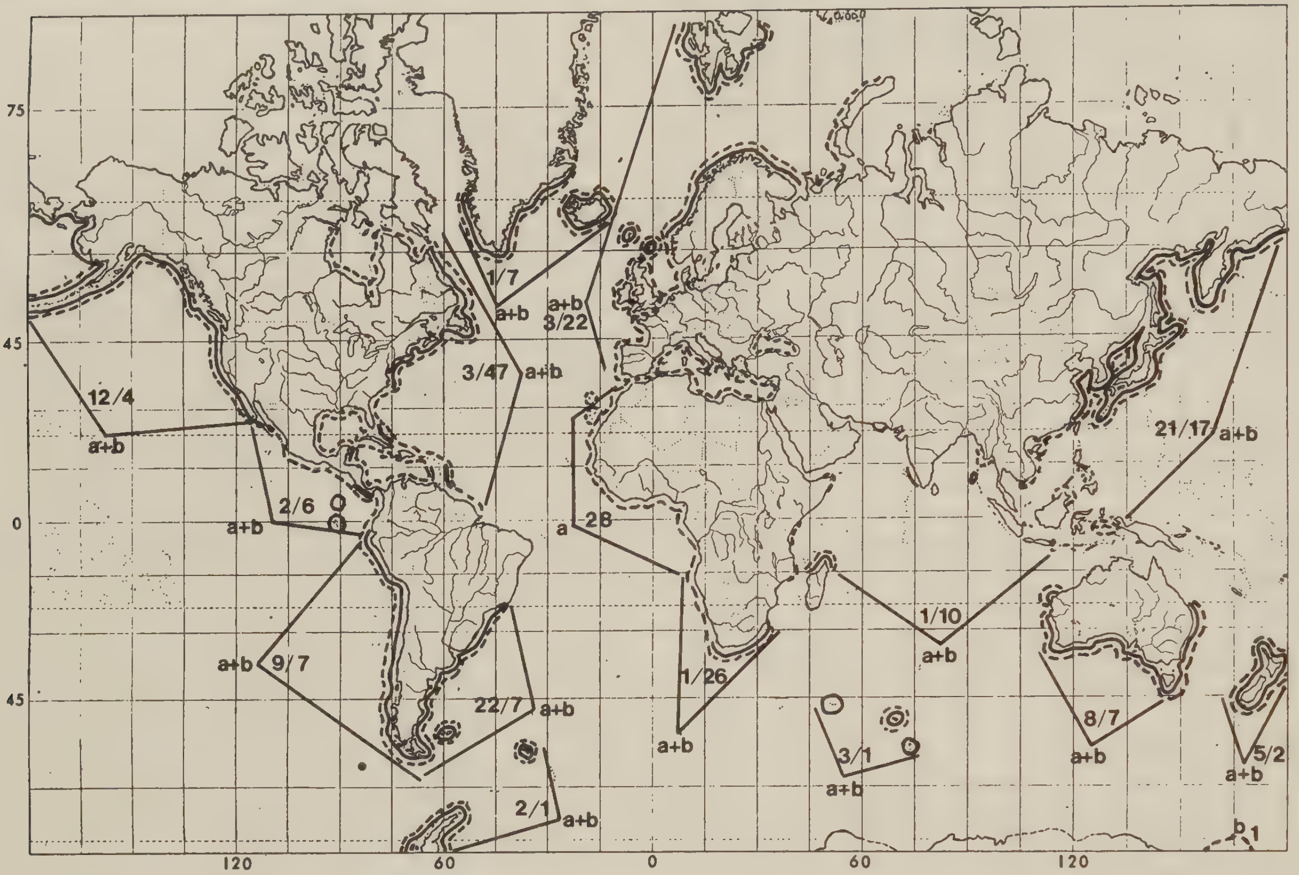

Figure 2.
Distribution of rajoid Group I and Group II. a = Group I; b = Group II; solid lines = range of Group I; dashed lines = range of Group II; numbers or numerators = number of species of Group I in specified areas; and numbers or denominators = number of species of Group II in specified areas. In some cases the same species occurs in more than one area and is counted more than once.

taxa and one outgroup (Rhinobatidae, *Rhinobatos*), and 34 anatomical characters. To facilitate the PAUP analysis the 29 recognized supraspecific taxa were reduced to 19 by combining supraspecific taxa with a complex synapomorphy which strongly suggested that they form a monophyletic group. The PAUP analysis revealed 45 most parsimonious trees and these were subjected to a strict consensus tree analysis (Swofford 1986) which resulted in a single tree (Fig. 1) resolved to the lowest level possible given the character matrix. The strict consensus tree was used in the zoogeographical and bathymetric analyses.

Zoogeographical and bathymetric data of all 224 to 227 species of skates were obtained from the literature (see McEachran and Miyake 1990) and from records accompanying specimens in the following museums: British Museum (Natural History), London; California Academy of Sciences, San Francisco; Field Museum of Natural History, Chicago; Florida State Museum, Gainesville; Kyoto University Research Station, Maizuru; Far Seas Fisheries Research Laboratory, Shimizu; Hokkaido University Museum, Hakodate; Los Angeles County Museum, Los Angeles; Museum of the Tokyo University of Fisheries, Tokyo; Universitat Hamburg Institut fur Seefischerei, Hamburg; Museum National d'Histoire Naturelle, Paris; Oregon State University Museum of Natural History, Corvallis; Oregon State University School of Oceanography, Corvallis; Texas Cooperative Wildlife Collection, College Station; National Museum of Natural History, Smithsonian Institution, Washington, D.C.; Scripps Institution of Oceanography Marine Vertebrate Collection, La Jolla; Virginia Institute of Marine Science, Gloucester Point; and Universiteit van Amsterdam Zoologisch Museum, Amsterdam. The entire skate collections of most of the institutions were surveyed.

The distributional data were analyzed phylogenetically. The range of geographical and bathymetric distribution was compiled for Group I and Group II, for all subgroups and for all supraspecific taxa of skates.

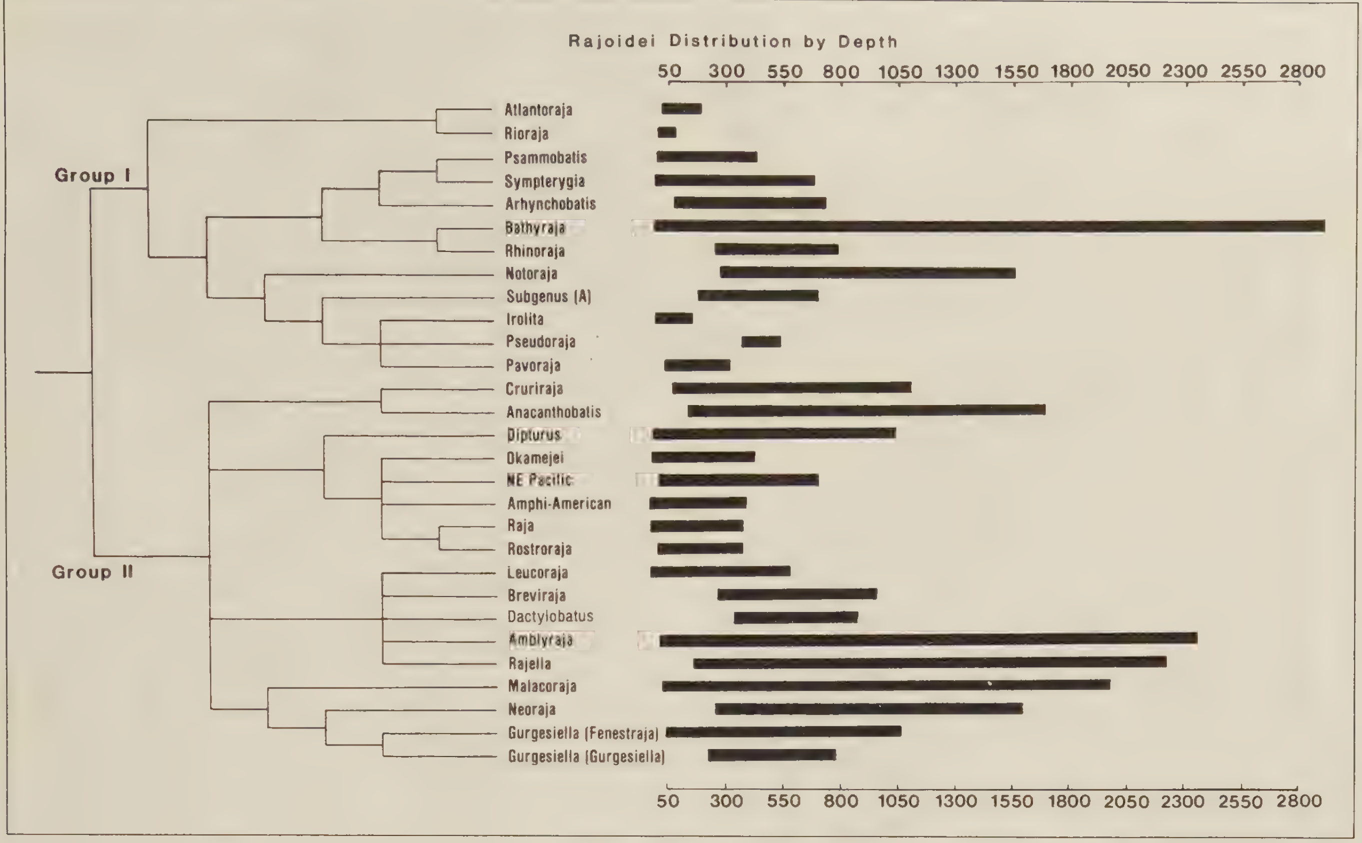

Figure 3.
Depth distribution of supraspecific taxa of Rajoidei in relation to hypothesis of relationships.

Results

The two major subdivisions of Rajoidei (Group I and Group II), considered familial level taxa by McEachran and Miyake (1990), have broadly overlapping geographical distributions (Fig. 2). Group I consists of 12 supraspecific taxa and about 79 species. Group II consists of 17 supraspecific taxa and about 145 to 148 species. Although the two groups broadly overlap, Group I is most diverse in the North Pacific and in the western South Atlantic, and Group II is most diverse in the North Atlantic and the eastern South Atlantic-western Indian Ocean. Group I is virtually absent from the North Atlantic, the eastern South Atlantic, and the northern Indian Ocean. Group I is more diverse than Group II at higher latitudes, and Group II is more diverse than Group I at lower latitudes. Both groups are of about equal diversity in the western North Pacific but in this area Group I predominates at higher latitudes, and Group II predominates at lower latitudes.

The two groups have broad overlapping depth ranges (Fig. 3). In fact, most supraspecific taxa have broad depth ranges and can be divided only into three general categories of depth distribution, shallow (to depths of 500 m), intermediate (to depths of 1500 m) and deep (to depths of 2900 m). However, Group II possesses more supraspecific taxa with broad depth ranges than does Group I. Only two supraspecific taxa of Group I have species which are recorded from depths greater than 1000 m.

The *Atlantoraja*-*Rioraja* clade is the sister group of the 10 other supraspecific taxa of Group I. It consists of *Raja* (*Atlantoraja*) (three species) and *R.* (*Rioraja*) (one species) and is endemic to the inshore waters of the western South Atlantic off southern Brazil, Uruguay, and northern Argentina (Fig. 4). *Raja* (*Atlantoraja*) and *R.* (*Rioraja*) share this area with eight species of their sister group, but these eight species (*Bathyraja* spp., *Psammobatis* spp., and *Sympterygia* spp.) generally occur in deeper water than the species of the *Atlantoraja*-*Rioraja* clade.

The sister group of the *Atlantoraja*-*Rioraja* clade consists of Subgroup Ia and Subgroup Ib. Subgroup Ia consists of five supraspecific taxa, has an antitropical distribution and is most diverse in the North Pacific and the western South Atlantic (Fig. 5). Subgroup Ia is allopatric with respect to its sister group, Subgroup Ib, except in the North Pacific, where it overlaps with one species of Subgroup Ib found off Japan, and in the temperate western South Pacific, where three species of *Bathyraja* and *Arhynchobatis asperimus* overlap with three supraspecific taxa of Subgroup Ib.

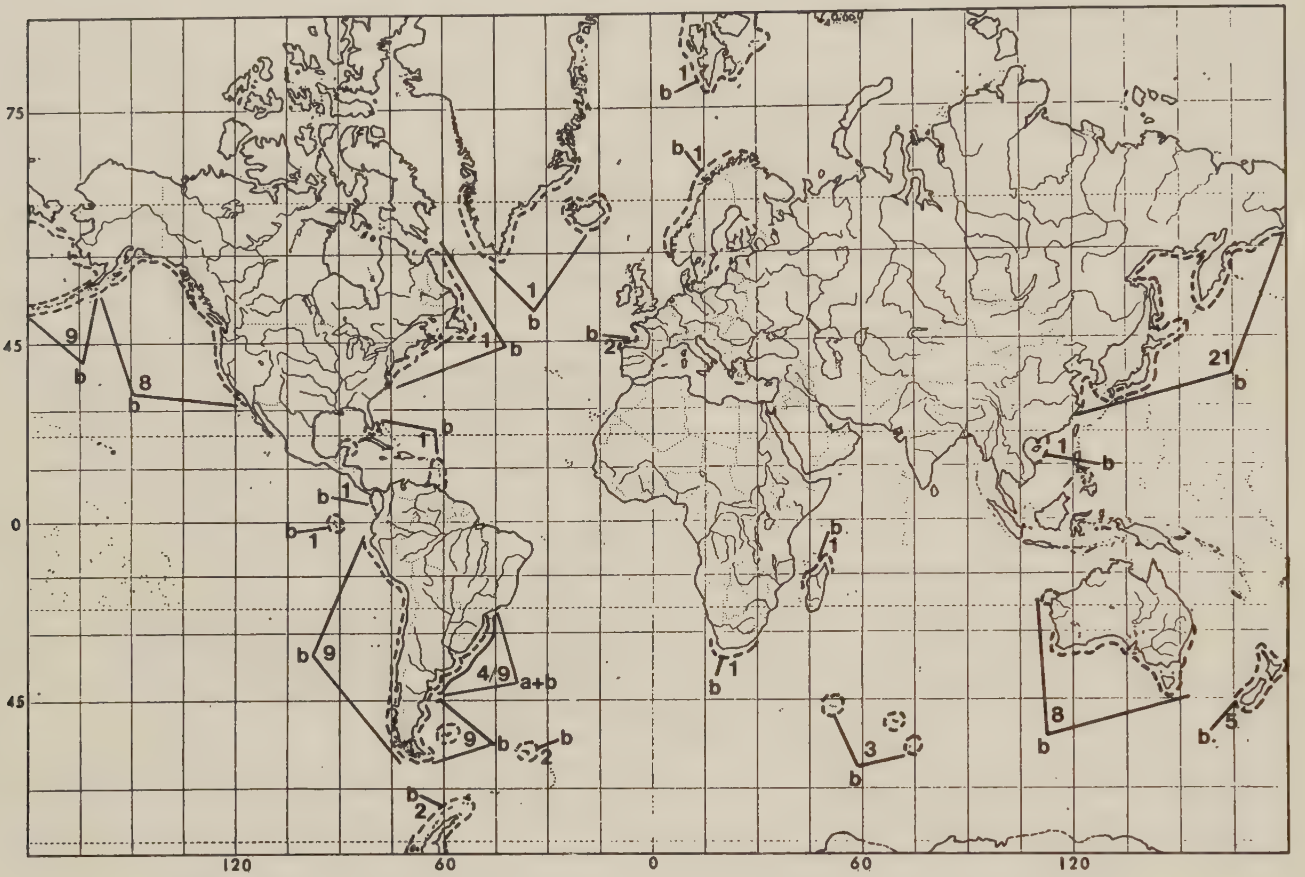

Figure 4.
Distribution of Group I. a = *Raja* (*Atlantoraja*) clade; b = Subgroup Ia (*Bathyraja*, *Psammobatis*, *Sympterygia*, and *Arhynchobatis*) and Subgroup Ib (*Notoraja*, Subgenus A, *Irolita*, *Pseudoraja*, and *Pavoraja*); solid lines = range of *R.* (*Atlantoraja*) and *R.* (*Rioraja*); dashed lines = range of Subgroup Ia and Subgroup Ib; numerator = number of species of *R.* (*Atlantoraja*) and *R.* (*Rioraja*) in designated area; and numbers or denominator = number of species of Subgroup Ia and Subgroup Ib in designated area. In some cases the same species occurs in more than one area and is counted more than once.

Within Subgroup Ia, the *Bathyraja–Rhinoraja* clade is the sister group of *Arhynchobatis*, *Psammobatis*, and *Sympterygia*. The former consists of *Bathyraja*, with about 45 species, and *Rhinoraja*, with four nominal species, and is allopatric with respect to its sister group except off temperate South American and around New Zealand. *Bathyraja* is largely antitropical and is most diverse in the North Pacific and the western South Atlantic (Fig. 6). *Bathyraja* is found over the entire depth range of skates (Fig. 3). The majority of the species occur at depths of less than 1000 m (Fig. 7). Only seven species are restricted to depths greater than 1000 m and can thus be considered deep-sea fishes. A majority of the species also have relatively small horizontal ranges; however, the two species which have been recorded from the greatest depths are widely distributed. *B. richardsoni* ranges from New Zealand in the western South Pacific to the Bay of Biscay off France (Forster 1965) and the Virginia Capes to southern Labrador (Templeman 1973) in the North Atlantic. *Bathyraja abyssicola* occurs along the northern rim of the North Pacific from central Japan to Baja, California (Zorzi and Anderson 1988). All four of the *Rhinoraja* species are distributed in the boreal western North Pacific. Three of these species are endemic to northern Japan and the other is endemic to Kamchatcka Peninsula in the western Bering Sea. All species of *Rhinoraja* occur in relatively shallow water.

The *Arhynchobatis–Psammobatis–Sympertygia* clade occurs sympatrically with the *Bathyraja–Rhinoraja* clade over its entire range but it is more restricted to shallow water than the latter (Fig. 3). *Arhynchobatis* is monotypic and endemic to New Zealand. The sister group of *Arhynchobatis* consists of *Psammobatis*, with eight species, and *Sympterygia*, with four species, and is endemic to temperate South America. One species of *Psammoabtis*, *P. scobina*, occurs in the eastern South Pacific off Chile, and seven species occur in the western South Atlantic. Four of the Atlantic species are

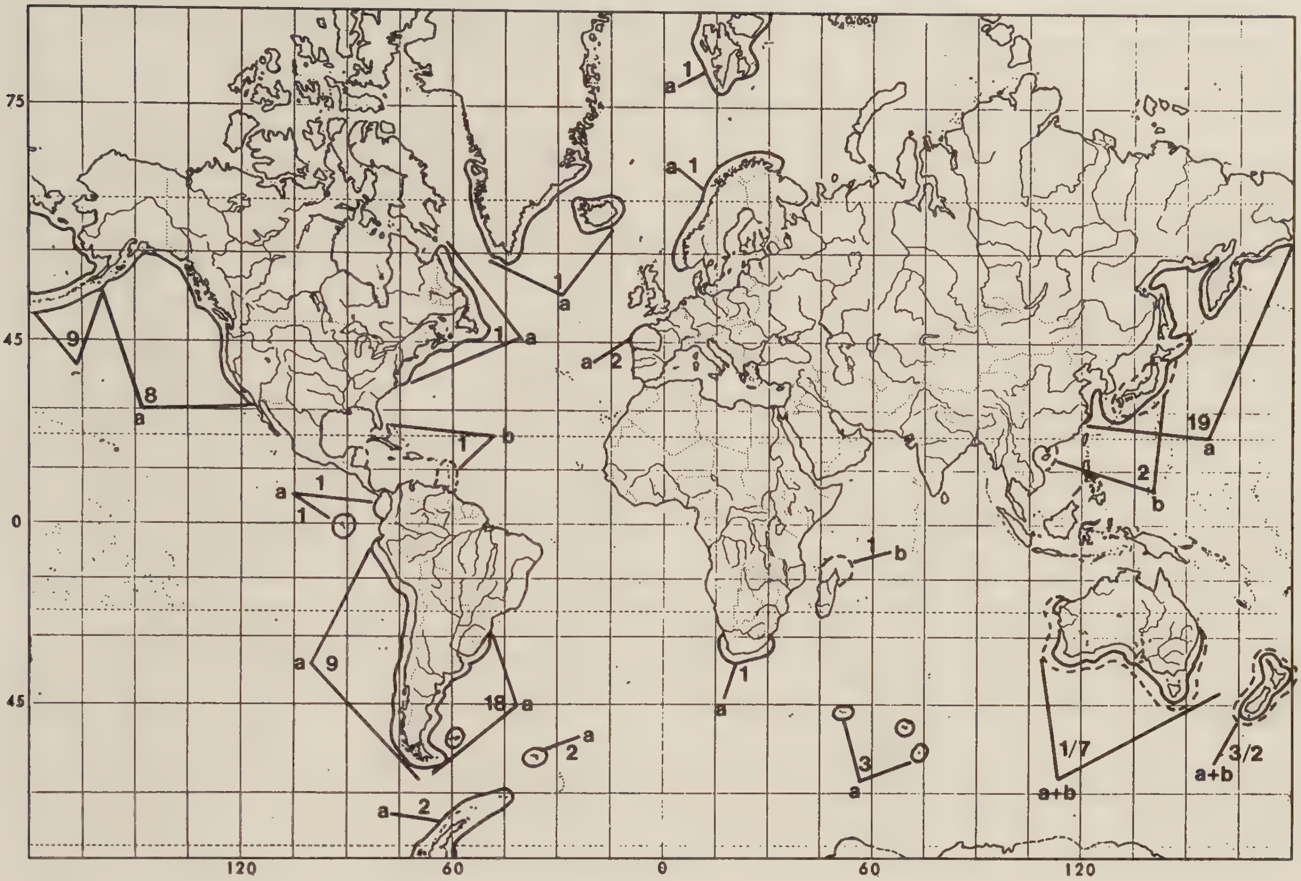

Figure 5.
Distribution of Group I (in part). a = Subgroup Ia (*Bathyraja*, *Rhinoraja*, *Psammobatis*, *Sympterygia*, and *Arhynchobatis*); b = Subgroup Ib (*Notoraja*, Subgenus A, *Irolita*, *Pseudoraja*, and *Pavoraja*); solid lines = range of Subgroup Ia; dashed lines = range of Subgroup Ib; numbers or numerators = number of species of Subgroup Ia in designated areas; and numbers or denominators = number of species of Subgroup Ib in designated areas. In some cases the same species occurs in more than one area and is counted more than once.

limited to the warm temperate region off southern Brazil, Uruguay and northern Argentina, two species extend from the southern section of the warm temperate region to the cold temperate region off southern Argentina and one species is known from only the Falkland Islands (McEachran 1983). Two of the *Sympterygia* species occur in the temperate eastern South Pacific and two occur in the western South Atlantic. One species of each pair is warm temperate and the other is cold temperate in distribution but both pairs are partially sympatric (McEachran 1982).

Subgroup Ib occurs in six widely separated areas, i.e., off temperate Australia, New Zealand, Madagascar, Japan, in the South China Sea, and in the Caribbean Sea (Figs. 5, 8). *Notoraja* is the sister group of the remainder of the subgroup and consists of three species which are allopatrically distributed with respect to each other and with respect to their sister group. *Notoraja tobitukai*, the only described species, occurs from Honshu, Japan to Okinawa, Japan (Nakaya 1984). The two undescribed species are endemic to either the South China Sea (Stehmann In press) or northern Madagascar (B. Seret, Museum Natl. d'Histoire Nat., Paris, pers. commun., February 1986). The three species are found at intermediate depths along the continental slope.

The sister group of *Notoraja* consists of an unnamed supraspecific taxon, Subgenus A, and its sister group, an unresolved trichotomy of *Irolita*, *Pseudoraja*, and *Pavoraja*. Subgenus A consists of two species, *Pavoraja asperula* and *P. spinifera*, which are endemic to the slope off New Zealand (Garrick and Paul 1974). The former species occurs along the upper slope, while the latter occurs along the middle slope. *Irolita* is monotypic and endemic to southern and western Australia where it broadly overlaps with *Pavoraja*. *Pavoraja* consists of six species which are endemic to western, southern, and eastern Australia (Last In press). Both *Irolita* and *Pavoraja* are found on the continental shelf.

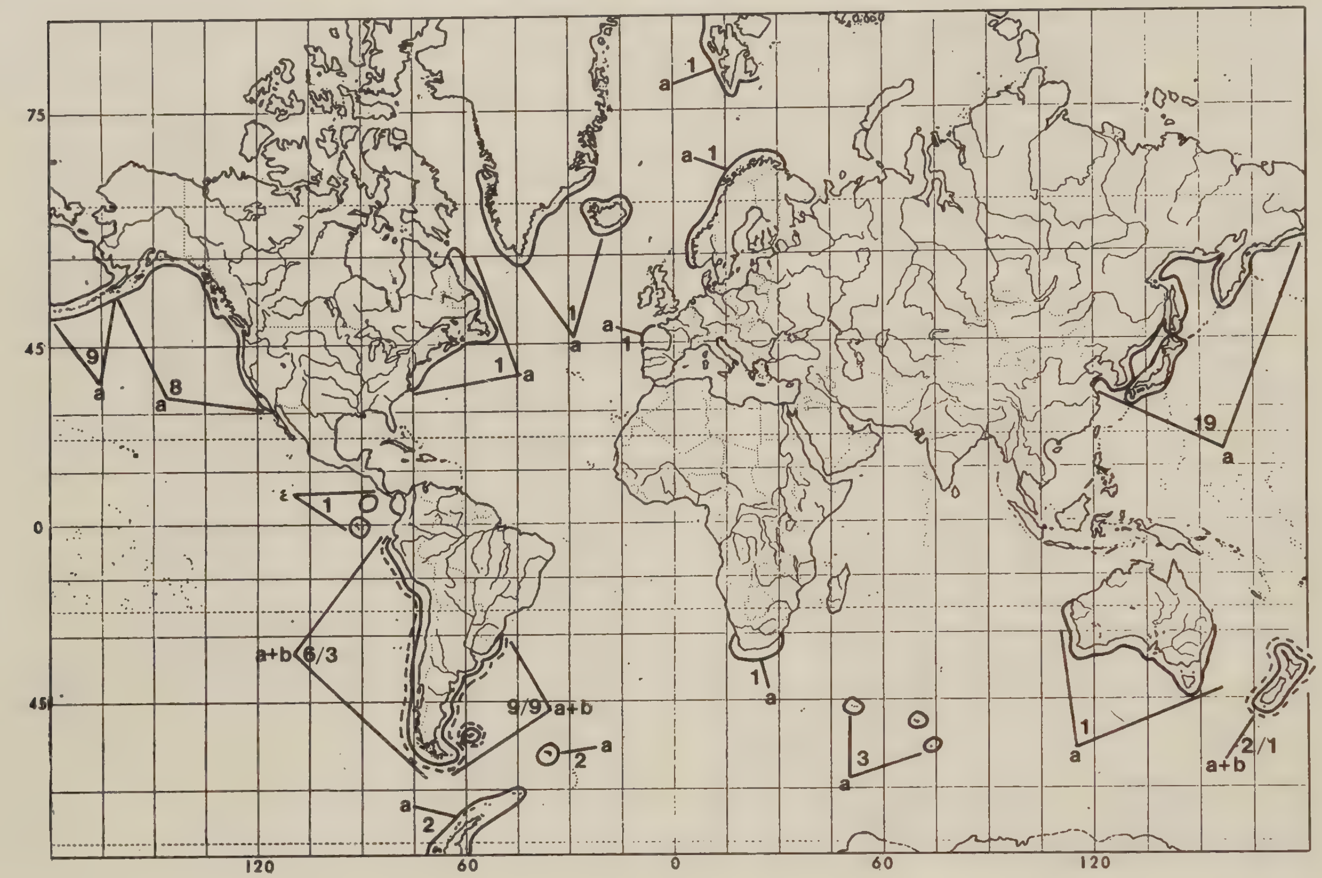

Figure 6.

Distribution of Subgroup Ia. a = *Bathyraja* and *Rhinoraja*; b = *Psammobatis*, *Sympterygia*, and *Arhynchobatis*; solid lines = range of *Bathyraja* and *Rhinoraja*; dashed lines = range of *Psammobatis*, *Sympterygia*, and *Arhynchobatis*; numbers or numerators = number of species of *Bathyraja* and *Rhinoraja* in designated areas; and numbers or denominators = number of species of *Psammobatis*, *Sympterygia*, and *Arhynchobatis* in designated area. In some cases the same species occurs in more than one area and is counted more than once.

Pseudoraja is monotypic and confined to the upper slope of the Caribbean Sea.

Group II consists of four subgroups with unresolved relationships (Fig. 1). Subgroup IIa, *Cruriraja* and *Anacanthobatis*, has a broad but disjunct tropical and warm temperate distribution (Fig. 9). *Cruriraja* consists of eight species, four of these are endemic to the tropical and warm temperate western North Atlantic, three are endemic to waters off southern Africa, and one is endemic to the northern Indian Ocean. *Anacanthobatis* consists of seven to ten species, three of these are endemic to the tropical and warm temperate western North Atlantic, two are endemic to the southwestern Indian Ocean and the remaining two to five species are endemic to the South China Sea or the East China Sea. Both *Cruriraja* and *Anacanthobatis* occur from the outer continental shelf to the mid or lower slope (Fig. 3), and species within each of the regions overlap to some degree.

Subgroup IIb consists of six supraspecific taxa of the genus *Raja* (*Dipturus*, *Okamejei*, *Raja*, *Rostroraja*, a North Pacific *Raja* assemblage, and an amphi-American *Raja* assemblage) and occurs nearly worldwide in tropical to temperate latitudes (Fig. 10). *Raja* (*Dipturus*) is the sister group of the remainder of the clade, consists of about 28 species and occurs nearly worldwide with exception of the tropical eastern and North Pacific and the tropical western Pacific. It is most diverse in the western North Atlantic, southern African region, and eastern North Atlantic but is poorly represented in the northern Indian Ocean and the western South Pacific. It broadly overlaps with its sister group in the Atlantic and western Pacific but is relatively more abundant at higher latitudes and at greater depths than its sister group. It occurs from the outer continental shelf to the lower slope, while its sister group is mostly confined to the outer continental shelf and upper slope (Fig. 3). Most of the species have broad depth ranges

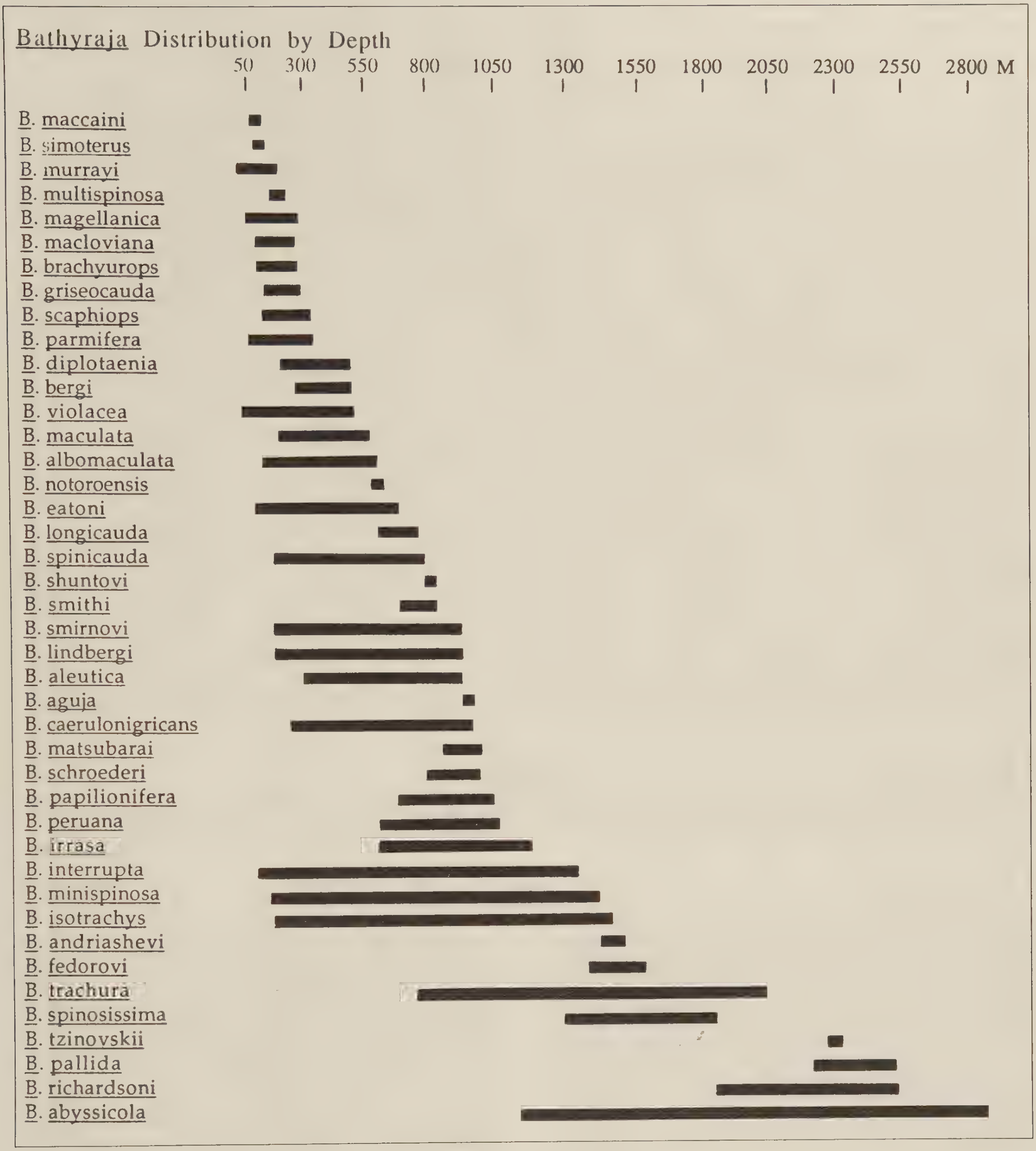

Figure 7.

Depth distribution of the species of *Bathyraja*. *Bathyraja ogilby*, *B. trachouros*, and *B.* sp. *Stehmann* were not included because of lack of depth information.

(Fig. 11). In tropical waters *R.* (*Dipturus*) species are generally found on the slope.

The interrelationships of the five taxa comprising the sister group of *R.* (*Dipturus*) have not been resolved (McEachran and Miyake 1986). Four of the five supraspecific groups are largely allopatrically or parapatrically distributed with respect to each other (Fig. 12). *Raja* (*Raja*), 14 species, and *R.* (*Rostroraja*), one species, co-occur over

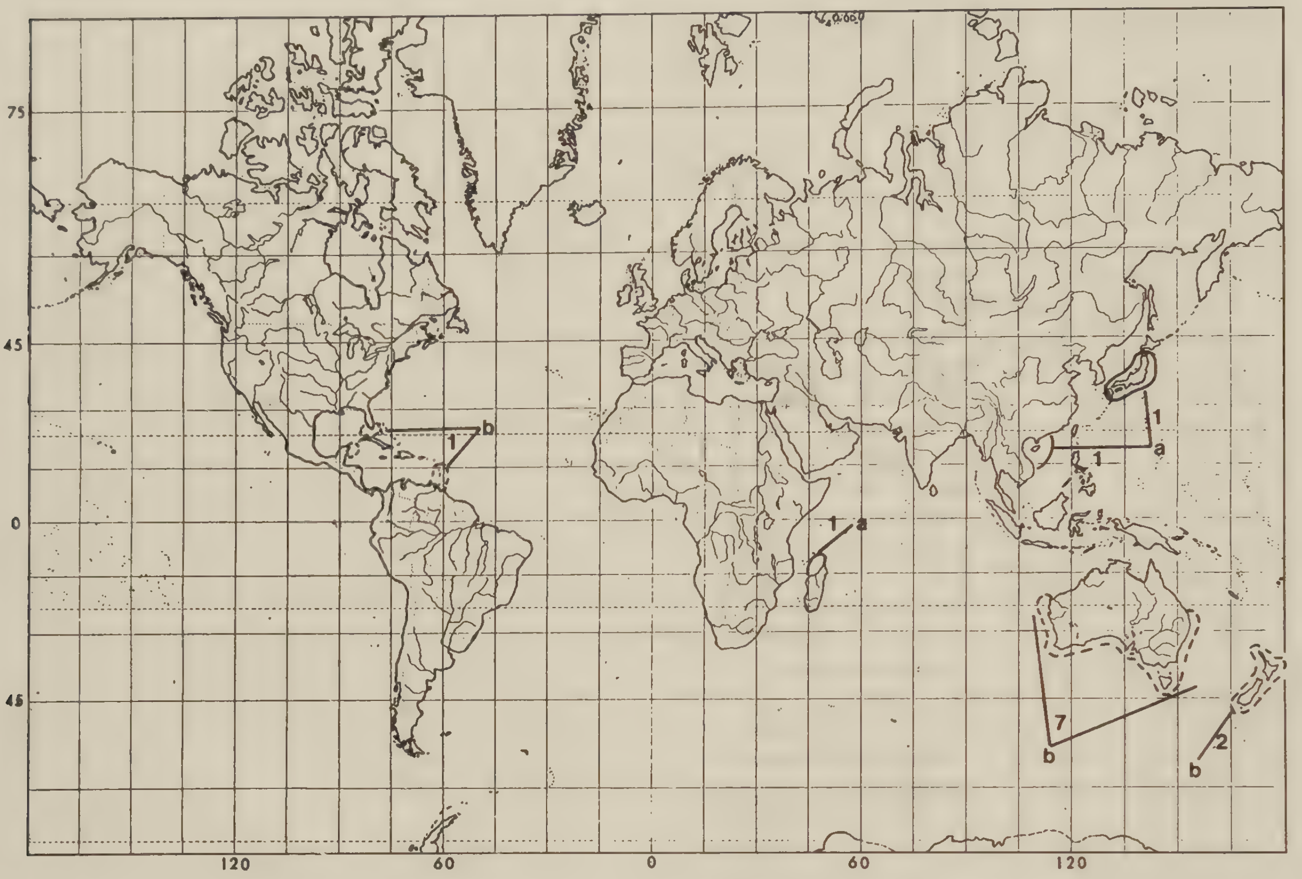

Figure 8.
Distribution of Subgroup Ib. a = *Notoraja*; b = Subgenus A, *Irolita*, *Pavoraja*, and *Pseudoraja*; solid lines = range of *Notoraja*; dashed lines = range of Subgenus A, *Irolita*, *Pseudoraja*, and *Pavoraja*; and numbers = number of species in designated areas.

almost their entire ranges but are allopatric with respect to the other three supraspecific taxa. *Raja* (*Raja*) occurs from Iceland and northern Norway to Natal, South Africa. *Raja* (*Rostroraja*) *alba* ranges from southwestern Ireland to northeastern Madagascar (Stehmann and Bürkel 1984). The greatest diversity of species occurs in the Mediterranean, where nine species of *R.* (*Raja*) and *R.* (*Rostroraja*) *alba* occur. Several of the species of *R.* (*Raja*) have fairly restricted ranges. Four species (*R. africana*, *R. asterias*, *R. polystigma*, and *R. radula*) are endemic to the Mediterranean; one species, *R. maderensis*, is endemic to Madeira and another species, *R. herwigi*, is endemic to the Cape Verde Islands (Stehmann and Bürkel 1984). Most of the species are confined to the continental shelf, five, in addition to *R.* (*Rostroraja*) *alba* also occur on the upper continental slope.

Raja (*Okamejei*) consists of 13 species and occurs in the tropical northern Indian Ocean, two species, and the tropical to warm temperate western Pacific, 11 species *Raja* (*Okamejei*) occurs allopatrically with respect to the other four supraspecific taxa except in the western North Pacific where it overlaps with one species of the North Pacific *Raja* assemblage. In the northern Indian Ocean, *R. heemstrai* occurs off Kenya and Tanzania (McEachran and Fechhelm 1982), *R. powelli* occurs in the Gulf of Aden and the Gulf of Martaban, Burma (Stehmann 1976), and three, possibly undescribed species of *R.* (*Okamejei*), occur off southern Indonesia (Gloerfelt-Tarp and Kailola 1984). In the western South Pacific five species of *R.* (*Okamejei*) occur off the western, southern, and eastern coasts of Australia. In the western North Pacific six species of *R.* (*Okamejei*) occur from the South China Sea to northern Japan (Ishiyama 1958; Ishihara 1987). Most of the species are confined to the continental shelf but a few also occur on the upper slope.

The North Pacific *Raja* assemblage consists of one species in the western North Pacific and five species in the eastern North Pacific. This assemblage broadly overlaps with *R.* (*Okamejei*) in the western North Pacific and slightly overlaps with the amphi-American *Raja* assemblage in the eastern North Pacific. The western North Pacific species, *Raja*

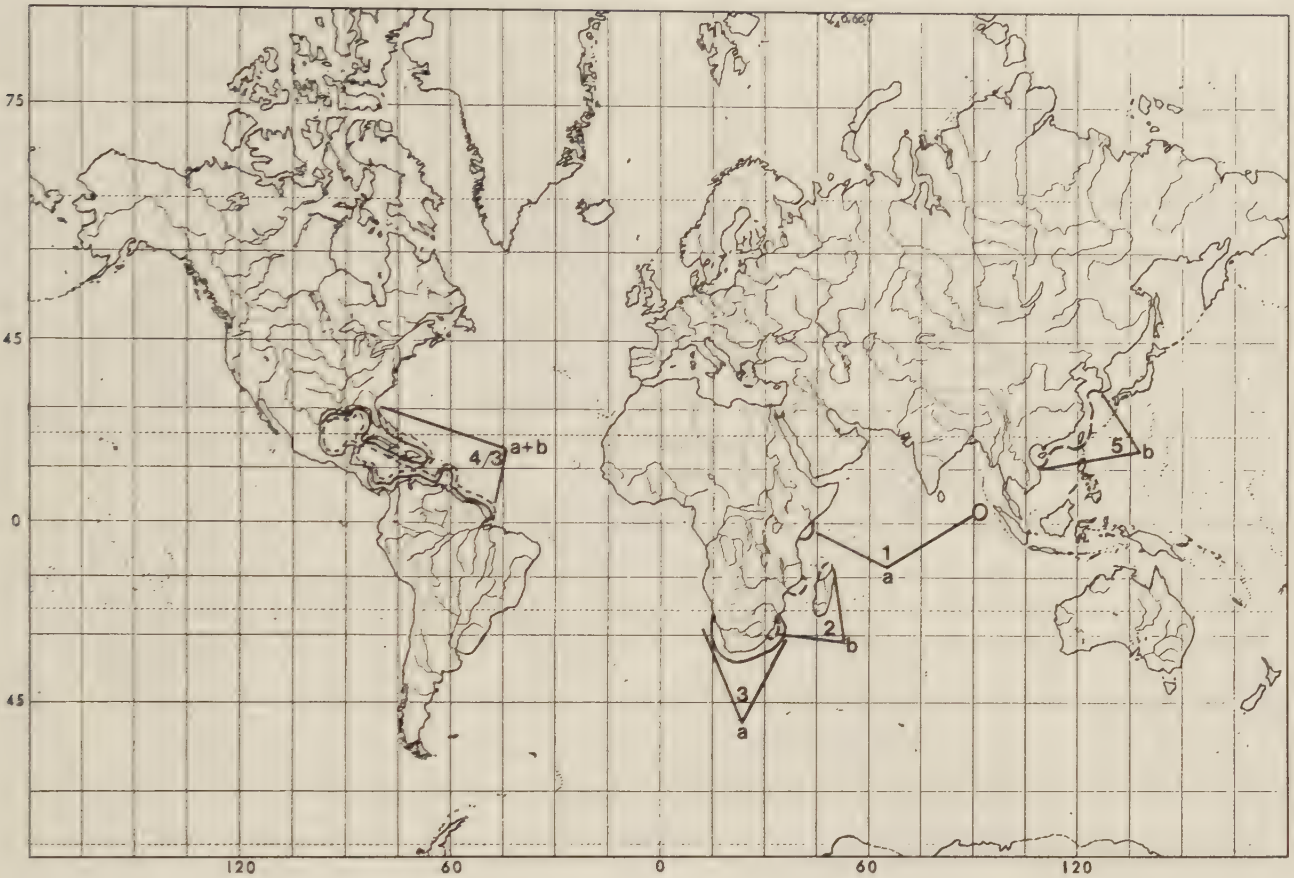

Figure 9.
Distribution of Subgroup IIa, *Cruriraja* and *Anacanthobatis*. a = *Cruriraja*; b = *Anacanthobatis*; solid lines = range of *Cruriraja*; dashed lines = range of *Anacanthobatis*; numbers or numerators = number of species of *Cruriraja* in designated areas; numbers or denominators = number of species of *Anacanthobatis* in designated areas.

pulchra, ranges from the East China Sea to Hokkaido, Japan and the Sea of Okhotsk. In the eastern Pacific, the North Pacific *Raja* assemblage extends from the Bering Sea to about midlength along the Baja Peninsula coast and also occurs in the Gulf of California. *Raja binoculata*, *R. inornata*, *R. rhina*, and *R. stellulata* occur along the western North American coast. *Raja inornata* and *R. rhina* also occur in the Gulf of California, and *R. cortezensis* is endemic to the Gulf of California (McEachran and Miyake 1988). Three of the species are limited to the continental shelf, while *R. inornata*, *R. rhina*, and *R. stellulata* extend from the continental shelf to the slope.

The amphi-American *Raja* assemblage consists of two species in the eastern tropical Pacific and five species in the tropical to warm temperate western North Atlantic. The eastern Pacific species, *R. equatorialis* and *R. velezi*, range from the Gulf of California, where they overlap with *R. cortezensis*, *R. inornata*, and *R. rhina*, to northern Peru. The five western Atlantic species are allopatric with respect to the four other supraspecific taxa and occur from Massachusetts to Yucatan, from the Bahamas to the northern coast of South America, and from Venezuela to Surinam. Four of these species have rather restricted ranges. *Raja ackleyi* occurs on the seaward and gulf sides of the Yucatan Peninsula. *Raja bahamensis* is endemic to the Bahamas. *Raja cervigoni* occurs from eastern Venezuela to Surinam. *Raja texana* is endemic to the northern Gulf of Mexico. The fifth species, *R. eglanteria*, is more widely distributed, it occurs from Cape Cod, Massachusetts to southern Florida and the northern Gulf of Mexico. Six of the seven species of the assemblage are limited to the continental shelf; *R. bahamensis* occurs along the upper insular slope.

Subgroup IIc consists of five supraspecific taxa, *Breviraja*, *Dactylobatus*, *R.* (*Amblyraja*), *R.* (*Leucoraja*), and *R.* (*Rajella*), is widely distributed from polar to tropical seas in the Atlantic and sparsely distributed in the Pacific and Indian oceans (Figs. 13, 14). Subgroup IIc is most diverse in the North Atlantic. Interrelationships within the clade

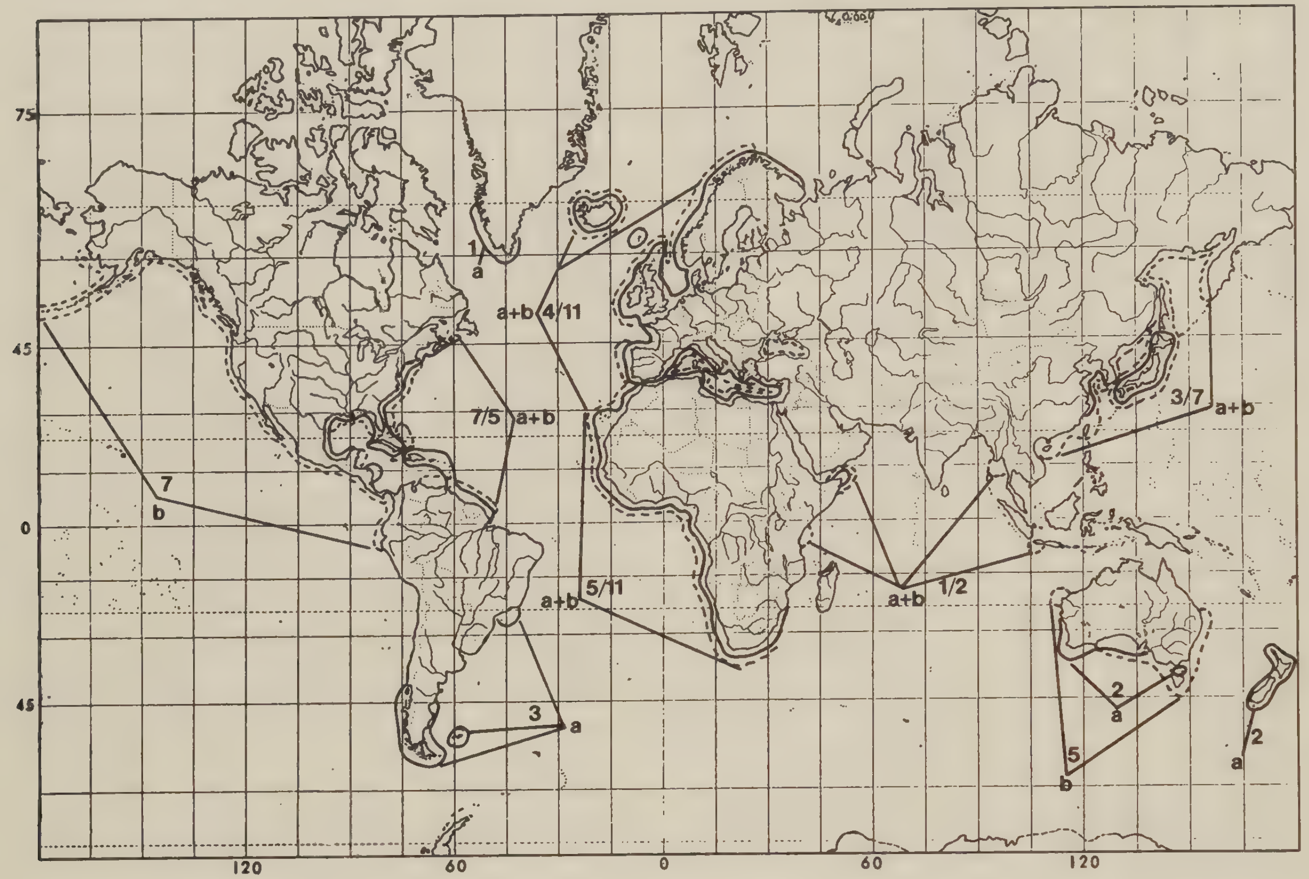

Figure 10.
Distribution of Subgroup IIb. a = *Raja* (*Dipturus*); b = *R.* (*Okamejei*), *R.* (*Raja*), *R.* (*Rostroraja*), North Pacific *Raja* assemblage, and amphi-American *Raja* assemblage; solid lines = range of *R.* (*Dipturus*); dashed lines = range of sister group of *R.* (*Dipturus*); numbers or numerators = number of species of *R.* (*Dipturus*) in designated areas; and numbers or denominators = number of species of sister group of *R.* (*Dipturus*) in designated areas. In some cases the same species occurs in more than one area and is counted more than once.

have not been resolved. *Raja* (*Amblyraja*) comprises nine species, and with the exception of *R. badia* and *R. reversa*, is restricted to polar and boreal or cold temperate waters. *Raja badia* occurs at abyssal depths from the tropical eastern Pacific off Panama northeastward to Hokkaido, Japan (Zorzi and Anderson 1988), and *R. reversa* occurs along the lower slope in the northern Indian Ocean (Stehmann 1976). *Raja* (*Amblyraja*) broadly overlaps with *R.* (*Leucoraja*) and *R.* (*Rajella*) in the North Atlantic and off South Africa but is allopatric with respect to the other four supraspecific taxa in the North Pacific, in the cold temperate western South Atlantic, off Antarctica, and in the northern Indian Ocean. Most of the species of *R.* (*Amblyraja*) have broad vertical distributions. *Raja hyperborea* and *R. jenseni* range from the edge of the continental shelf to about 2460 m.

Dactylobatus consists of two species endemic to the tropical and warm temperate western North Atlantic. Both species occur from the southeastern Florida coast throughout the Gulf of Mexico to northern South America, but *D. armatus* occurs along the upper half of the slope, while *D. clarki* occurs along the lower half of the slope. *Dactylobatus* overlaps with several species of *Breviraja* and with two species *R.* (*Leucoraja*) along the southeastern Florida coast and in the Caribbean and with one species of *R.* (*Leucoraja*) and two species of *R.* (*Rajella*) in the Gulf of Mexico.

Breviraja consists of six species which occur along the slope in the western North Atlantic from Nova Scotia to the Amazon. *Breviraja* overlaps with *R.* (*Amblyraja*) and *R.* (*Rajella*) off Nova Scotia and with *Dactylobatus* and *R.* (*Leucoraja*) off the southeastern United States and in the Caribbean. Most of the species of *Breviraja* are allopatric or parapatric with respect to their congeners and apparently none occur in the Gulf of Mexico (McEachran and Miyake 1987).

Raja (*Leucoraja*) consists of 10 species from the North Atlantic and eastern South Atlantic (Fig. 14). *Raja* (*Leuco-*

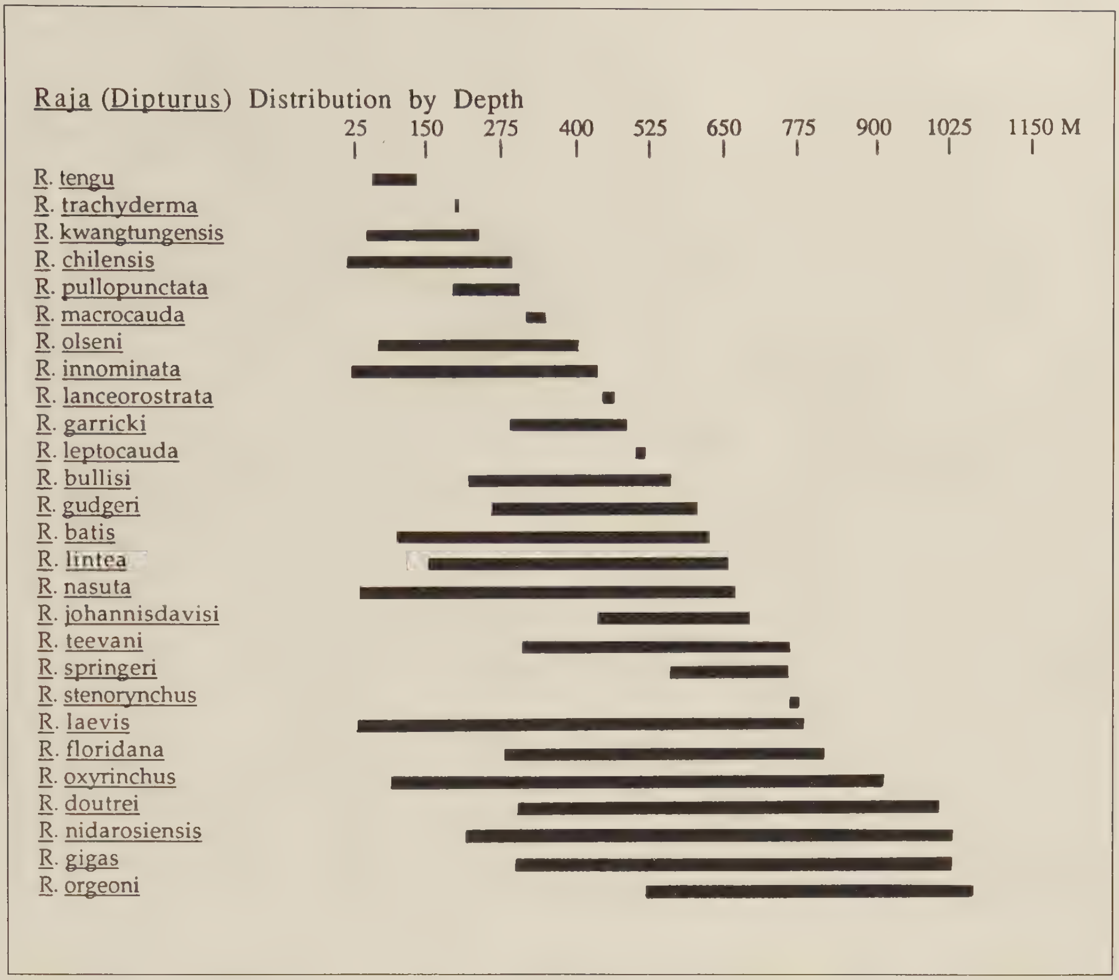

Figure 11.
Depth distribution of *R.* (*Dipturus*) species. *Raja whitleyi* was not included because of lack of depth information.

raja) broadly overlaps with *R.* (*Rajella*) and *R.* (*Amblyraja*) but is more restricted to lower latitudes and to the continental shelf and upper slope than the latter two subgenera, and it occurs allopatrically in the Mediterranean. Most of the species are found in warm temperate waters of the eastern North Atlantic. Three species of *R.* (*Leucoraja*) have rather restricted ranges, i.e., *R. melitensis* is endemic to the Mediterranean, *R. wallacei* is found off South Africa, and *R. yucatanensis* occurs off the east coast of Yucatan.

Raja (*Rajella*) consists of 14 species which occur in the North Atlantic, in the western South Atlantic, off southern Africa, in the northern Indian Ocean, and in the eastern South Pacific. *Raja* (*Rajella*) broadly overlaps the four other supraspecific taxa in the North Altantic and eastern South Atlantic but occurs at greater depths and at higher latitudes than all of these taxa, except *R.* (*Amblyraja*), and occurs allopatrically with respect to these taxa in the western South Atlantic, in the eastern South Pacific, and in the northern Indian Ocean. Highest species diversity occurs in the eastern South Atlantic. The species of *R.* (*Rajella*) are most frequently caught over the mid to lower slope.

Subgroup IId consists of four supraspecific taxa, *Malacoraja*, *Neoraja*, *Gurgesiella* (*Fenestraja*), and *G.* (*Gurgesiella*), and is widely distributed in the Atlantic but also occurs in the Indian Ocean and in the eastern South Pacific (Fig. 15). *Malacoraja* is the sister group of the three other taxa (McEachran 1984) and consists of three species endemic to the boreal and southern cold temperate Atlantic. Two of these species, *R. kreffti* and *R. spinacidermis*, are limited to the continental slope, and the latter occurs in both the North and eastern South Atlantic. The third species, *R. senta*, is found along the outer continental shelf and slope in the boreal western North Atlantic. *Malacoraja* overlaps with its sister group only off South Africa.

Neoraja is the sister group of *Gurgesiella* (*Gurgesiella*) and *G.* (*Fenestraja*) and consists of four species allopatrically distributed in the warm temperate western North Atlantic, temperate eastern North Atlantic, tropical eastern

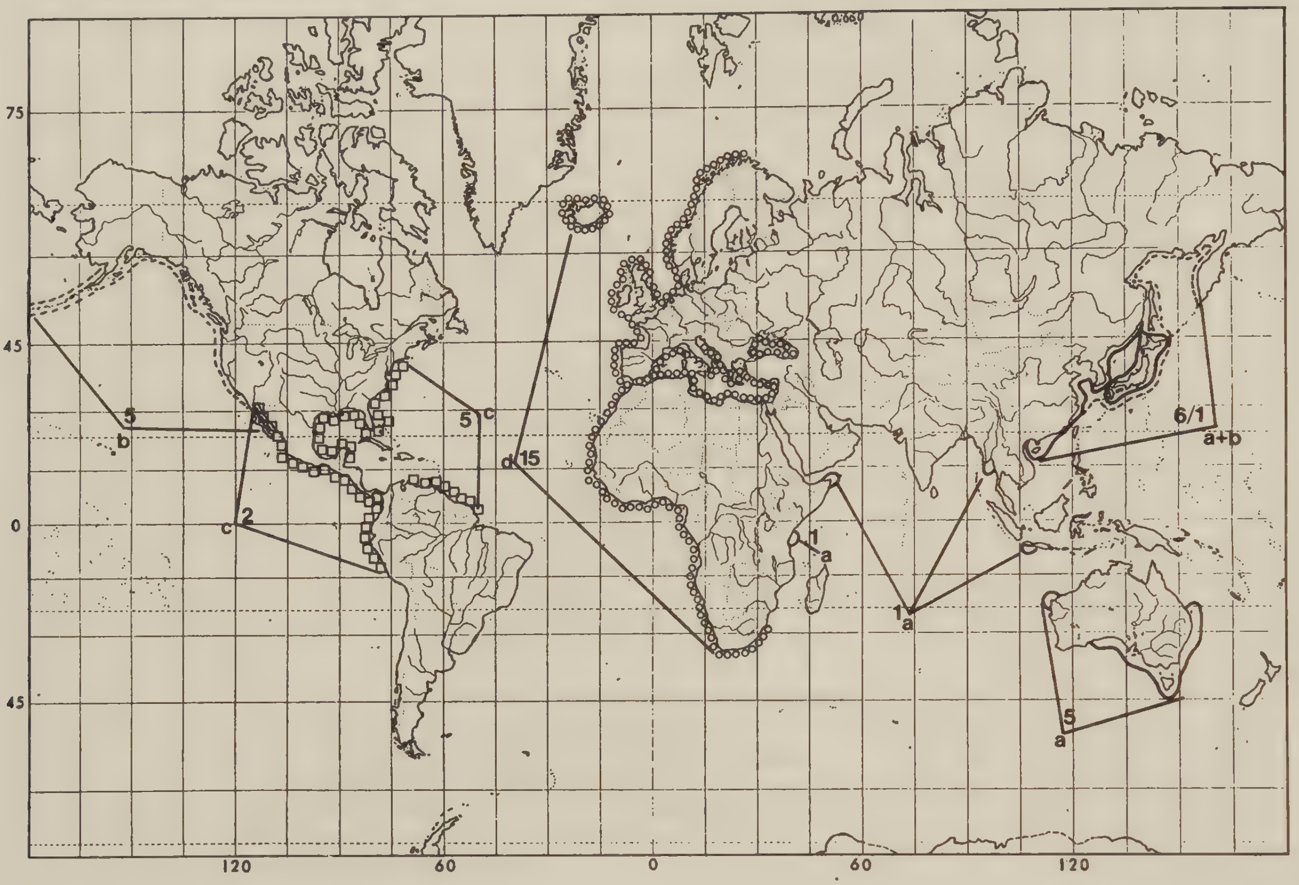

Figure 12.
Distribution of Subgroup IIb (in part). a = *R.* (*Okamejei*); b = North Pacific *Raja* assemblage; c = amphi-American *Raja* assemblage; d = *R.* (*Raja*) + *R.* (*Rostroraja*); solid lines = range of *R.* (*Okamejei*); dashed lines = range of North Pacific *Raja* assemblage; open squares = range of amphi-American assemblage; open circles = range of *R.* (*Raja*) + *R.* (*Rostroraja*); numbers = numbers of species in designated areas; numerator = number of species of *R.* (*Okamejei*) in designated area; and denominator = number of species of the North Pacific *Raja* assemblage in designated area.

Atlantic, and warm temperate eastern South Atlantic. *Neoraja* overlaps with its sister group only off the southeastern United States. All species of *Neoraja* occur along the slope between depths of 292 to 1262 m (McEachran and Stehmann 1984).

Gurgesiella (*Fenestraja*) consists of seven nominal species and one undescribed species. Five of the species are endemic to the tropical and warm temperate western North Atlantic, two are endemic to the northern Indian Ocean, and the undescribed species is from the southwestern Indian Ocean off Madagascar (B. Seret, ORSTROM, Museum Natl. d'Histoire Nat., Paris, written pers. commun., 1987). *Gurgesiella* (*Fenestraja*) overlaps with *G.* (*Gurgesiella*) only off Central American and northern South America. All species of *G.* (*Fenestraja*) are distributed along the outer continental shelf and slope.

Gurgesiella (*Gurgesiella*) consists of three species which are allopatrically distributed in the tropical western North Atlantic, warm temperate, and tropical western South Atlantic and warn temperate eastern South Pacific. All three species are found along the slope at depths ranging from 247 to 960 m (McEachran and Compagno 1980).

Discussion

Skate distributions form a number of zoogeographical patterns when examined from a phylogenetic perspective. Group I and Group II overlap broadly but have different centers of abundance. Group I occurs almost exclusively in the Pacific and in the western South Atlantic, while Group II occurs predominately in the North Atlantic, eastern South Atlantic-western Indian Ocean and the western Pacific.

Within Group I the *Raja* (*Atlantoraja*)–*R.* (*Rioraja*) clade is limited to the warm temperate western South Atlantic,

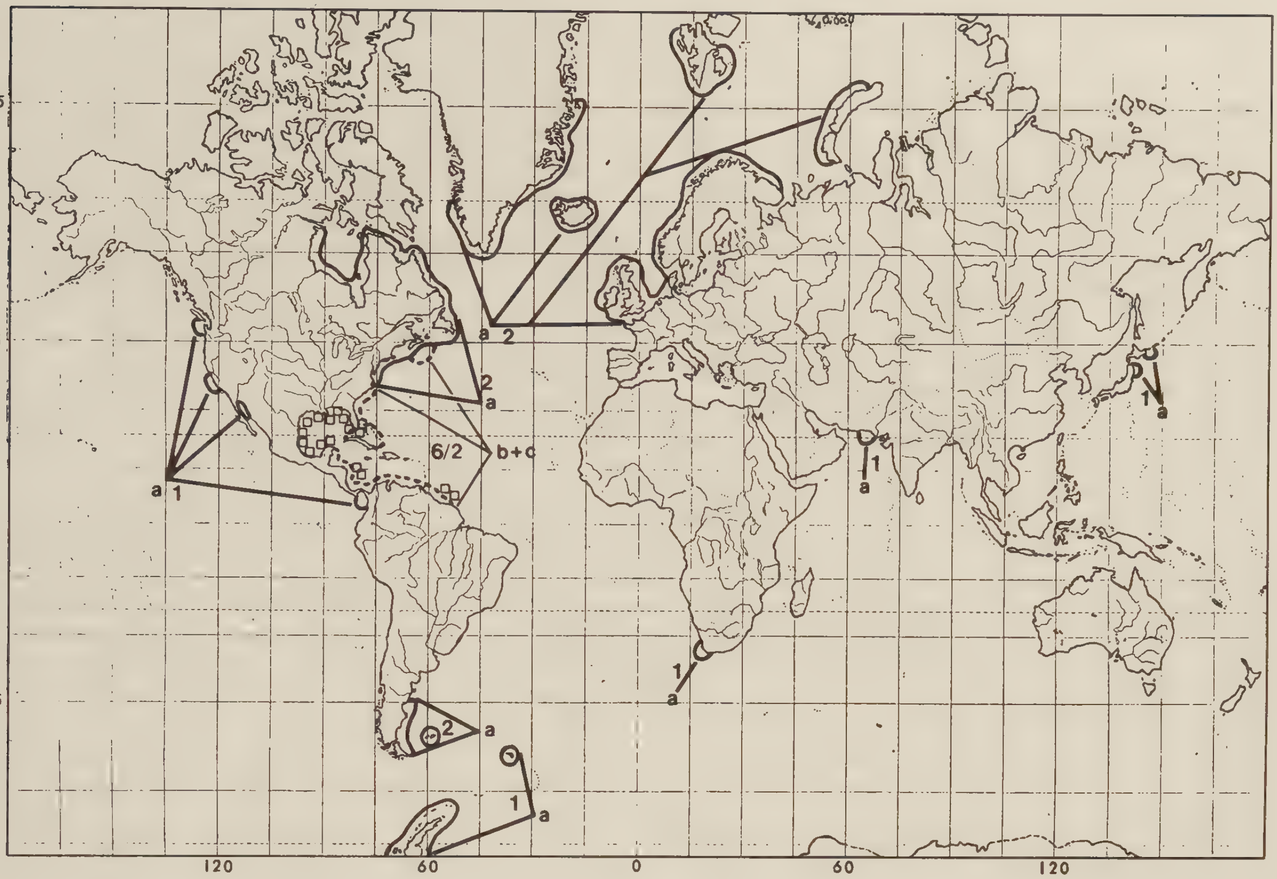

Figure 13.
Distribution of Subgroup IIc (in part). a = *R.* (*Amblyraja*); b = *Breviraja*; c = *Dactylobatus*; solid lines = range of *R.* (*Amblyraja*); dashed lines = range of *Breviraja*; open squares = range of *Dactylobatus*; numbers = number of species in designated areas; numerator = number of species of *Breviraja* in designated area; and denominator = number of species of *Dactylobatus* in designated area. In some cases the same species occurs in more than one area and is counted more than once.

while its sister group, Subgroup Ia and Subgroup Ib, ranges throughout the Pacific, southern Indian Ocean, and western South Atlantic. Subgroup Ia is largely antitropical in the Pacific and is warm temperate to polar in the Southern Hemisphere. *Bathyraja* has three centers of diversity, i.e., in the North Pacific, off temperate South America, and in the subantarctic and Antarctic waters (Stehmann 1986), while its sister group, *Psammobatis*, *Sympterygia*, and *Arhynchobatis*, is limited to temperate South America and New Zealand.

Subgroup Ib has a tropical to warm temperate distributional track, extending from the southwestern Indian Ocean to the northeastern Indian Ocean, to the western Pacific and the western North Atlantic. The western North Atlantic distribution is disjunct from the remainder of the track. *Notoraja* occurs in the tropical to warm temperate Indo-West Pacific while its sister group, Subgenus A, *Irolita*, *Pavoraja*, and *Pseudoraja*, is limited to the southern temperate region and the tropical western North Atlantic. Subgenus A is endemic to New Zealand, while its sister group occurs off Australia (*Irolita* and *Pavoraja*) and in the Caribbean Sea (*Pseudoraja*).

Group II displays four distributional patterns. Subgroup IIa, *Cruriraja* and *Anacanthobatis*, and *Gurgesiella* (*Fenestraja*) of Subgroup IId have a distributional track extending from the tropical western North Atlantic to the warm temperate eastern South Atlantic-southwestern Indian Ocean, to the tropical Indian Ocean-tropical to warm temperate western North Pacific. This is considered a distributional track for these three taxa, although each is missing from part of the track. *Anacanthobatis* is unreported from eastern South Atlantic and the tropical eastern Indian Ocean. *Cruriraja* is unknown from the western North Pacific. *Gurgesiella* (*Fenestraja*) has not been reported from the eastern South Atlantic and the western North Pacific.

Subgroup IIb has a circum-tropical-temperate distributional track. *Raja* (*Dipturus*) is circum-tropical-temperate, with exception of the tropical western Pacific and the

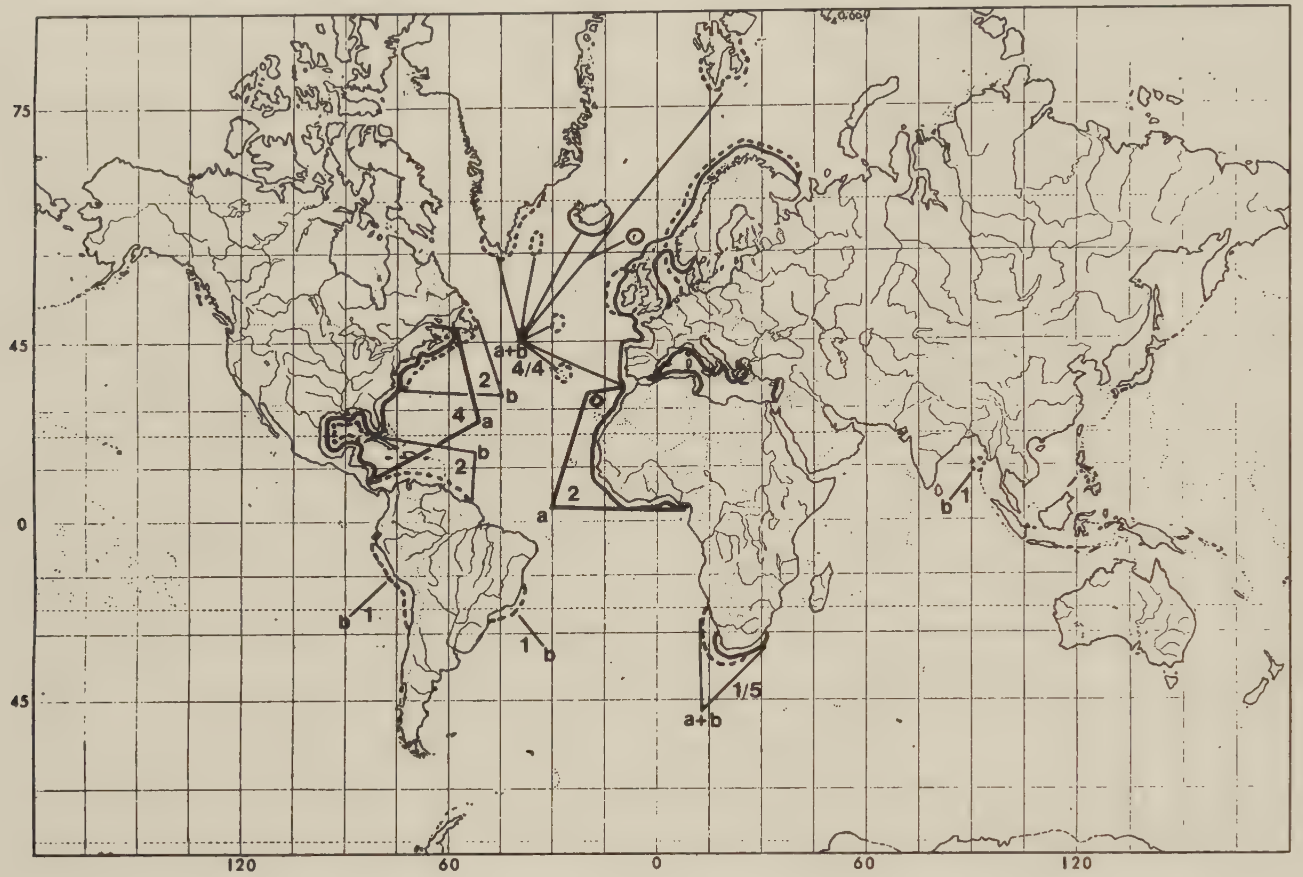

Figure 14.
Distribution of Subgroup IIc (in part). a = *R.* (*Leucoraja*); b = *R.* (*Rajella*); solid line = range of *R.* (*Leucoraja*); dashed line = range of *R.* (*Rajella*); numbers or numerators = number of species of *R.* (*Leucoraja*) in designated area; and denominators or numbers = number of species of *R.* (*Rajella*) in designated area. In some cases the same species occurs in more than one area and is counted more than once.

tropical and warm temperate eastern Pacific. Beebe and Tee Van (1941) reported a species, *R. ecuadoriensis*, which may be a representative of *R.* (*Dipturus*), from the tropical eastern Pacific; however, no specimens of this nominal species are available for study. The sister group of *R.* (*Dipturus*) is circum-tropical-warm temperate, and each of the four supraspecific taxa more or less restricted to one of the four major subdivisions of the tropical shore regions of the world (Briggs 1974). In the western Atlantic, eastern Atlantic, and western Pacific, *R.* (*Dipturus*) occurs at higher latitudes and at greater depths than its sister group.

Subgroup IIc, and *Malacoraja* and *Neoraja* of Subgroup IId, are largely limited to the Atlantic. *Raja* (*Amblyraja*), *R.* (*Rajella*), *Malacoraja*, *Neoraja*, and, to a lesser extent, *R.* (*Leucoraja*) display antitropical distributions. *Raja* (*Amblyraja*), *R.* (*Rajella*), *Malacoraja*, and *Neoraja* occur at the highest latitudes and the greatest depths, while *Breviraja* and *Dactylobatus* are limited to the tropical and temperate western North Atlantic.

Gurgesiella (*Gurgesiella*) of Subgroup IId has a unique amphi-South American distribution. The two Atlantic species are considered sister species and the sister group of the eastern South Pacific species (McEachran and Compagno 1980).

The distributional patterns outlined above, to a large extent, may reflect tectonic events which commenced in the Mesozoic. The Atlantic Ocean began to form in the Jurassic, South America and southern Africa began to separate in the Cretaceous and the Atlantic was fully formed latitudinally by the late Cretaceous (Hallam 1981). However, the Atlantic may have had only one deep-sea connection with the other oceans until the Eocene. A tropical sea, Tethys Sea, extended from the western Pacific to the proto-Atlantic, or possibly to the eastern Pacific, during the Triassic, but with breakup of Gondwanaland, it was restricted by collisions between the northern edges of Africa, Arabia, Iran, and India with southern edges of Eurasia during the Cretaceous and early Tertiary (Audley-

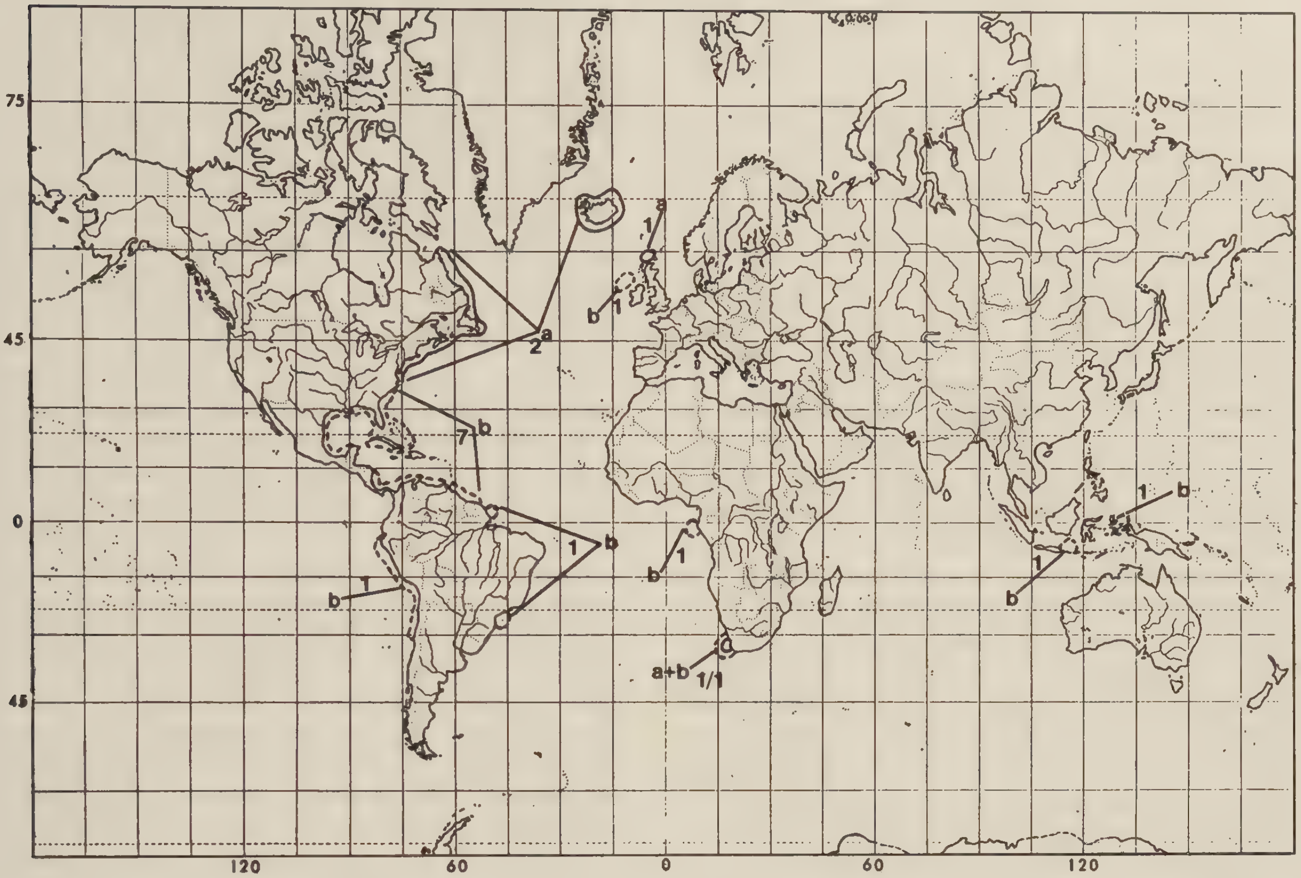

Figure 15.
Distribution of Subgroup IId. a = *Malacoraja*; b = *Neoraja*, *Gurgesiella* (*Fenestraja*), and *G.* (*Gurgesiella*); solid line = range of *Malacoraja*; dashed line = range of *Neoraja*, *G.* (*Fenestraja*), and *G.* (*Gurgesiella*); numbers or numerator = number of species in designated areas; and numbers or denominator = number of species of *Neoraja*, *G.* (*Fenstraja*), and *G.* (*Gurgesiella*) in designated area. In one case the same species occurs in more than one area and is counted more than once.

Charles et al. 1981). The Tethys was closed completely in the Oligocene to early Miocene (Hallam 1981). The southwestern entrance to the Atlantic is thought to have been partially restricted by the proximity of the Antarctic Peninsula and Tierra Del Fuego, and the Scotian ridge and islands which were situated between them until the Eocene (Norton and Sclater 1979). In the Eocene distance between South America and Antarctic widened and the Scotian ridge moved to the east (Norton and Sclater 1979). The northern entrance was restricted by the proximity of North America, Greenland, and Eurasia. Probably the only deep-sea entrance during the Cretaceous and early Tertiary was between the southeastern Atlantic and the southwestern Indian Ocean, between southern Africa and Antarctica (Norton and Sclater 1979). The southern continents assumed their present positions in the early Tertiary (Hallam 1981).

Skates date back to the Cenomanian of the Cretaceous of Europe, the Near East, and West Africa (Cappetta 1987) but probably originated contemporarily with or prior to the origin of the Atlantic. These early skate remains were most likely laid down in the Tethys Sea at the time of its diminution. Because of the vagaries of fossil formation and low probability of their subsequent discovery, the fossil record is only a minimal record of the age of a taxon (Hennig 1966), and thus skates are likely to be considerably older than the Cenomanian.

It is therefore likely that skates evolved in the Pacific and later dispersed into the Atlantic by means of one or more of the passages into the Atlantic from the Pacific or Indian oceans. Below we describe possible scenarios of how skates arrived at their present distribution under the premise that they evolved in the Pacific Ocean.

Group I has undergone most of its evolution along the rim of the Pacific basin and on the margins of the subantarctic and Antarctic land masses and plateaus. Ancestors of the *R.* (*Atlantoraja*)–*R.* (*Rioraja*) clade dispersed from shallow waters of the eastern South Pacific through the narrow passage into the Atlantic between the Antarctic Peninsula and Tierra del Fuego in the Cretaceous to early Tertiary and vicariated along the coasts of northern Argentina, Uruguay, and southern Brazil.

Subgroup Ia apparently had three centers of diversification: the northern Pacific, Patagonia, and the subantarctic–Antarctic region. In the North Pacific the ancestral form gave rise to a large number of *Bathyraja* species and to *Rhinoraja*. In the eastern South Pacific, an ancestral form gave rise to several *Bathyraja* species and to *Psammobatis* and *Sympterygia*, and all three supraspecific taxa dispersed into the western South Atlantic. The dispersal may have followed the broadening and deepening of the passage between the Antarctic Peninsula and Tierra del Fuego in the Eocene. These groups, especially *Bathyraja* and *Psammobatis*, underwent major radiations in the temperate western South Atlantic. The most derived species of *Psammobatis* and *Sympterygia* occur in the western South Atlantic (McEachran 1982, 1983). In the subantarctic and Antarctic region, an ancestral form gave rise to the *Bathyraja* species of the islands and plateaus of the subantarctic, to those of the Antarctic, New Zealand, Australia, and South Africa, and to *Arhynchobatis* from New Zealand. The *Bathyraja* fauna of southern Chile, Argentina, and the Falkland Islands may be a combination of the Patagonian and subantarctic–Antarctic stock. This scenario implies that *Bathyraja* is paraphyletic because separate lineages of this taxon are sister groups with *Rhinoraja*, *Psammobatis*, *Sympterygia*, and *Arhynchobatis*. This is not unlikely because *Bathyraja* is undefined by unique derived character states.

Subgroup Ib has undergone most of its evolution in the tropical and warm temperate Indo-Pacific. The *Notoraja*-like ancestoral clade may have arrived at its Indo-West Pacific distributional track early in the Tertiary, before separation of Antarctic, New Zealand, and Australia, and may have given rise to Subgenus A, *Irolita*, and *Pavoraja* on temperate regions of this supercontinent. Subgroup Ib also gave rise to the tropical western North Altantic taxon *Pseudoraja*. *Pseudoraja* may have evolved from Subgenus A stock that dispersed into the Atlantic with opening of the deep-sea connection between the eastern Pacific and western Atlantic in the Upper Paleocene (Hallam 1981). Alternatively, *Pseudoraja* may have evolved from Subgenus A stock which dispersed into the Atlantic from the Indian Ocean between southern Africa and Antarctica. This scenario would result in a similar track to those of *Anacanthobatis*, *Cruriraja*, and *G.* (*Fenestraja*).

Most of the evolution of Group II appears to have occurred in the North Atlantic, eastern South Atlantic–southwestern Indian Ocean, and Tethys Sea. Group II has four major tracks associated with creation of the Atlantic Ocean. Subgroup IIb has a Tethys Sea distributional track. The ancestor of this clade most likely assumed its distribution along tropical to temperate continental margins of the Atlantic, Indian Ocean, and western Pacific before the closure of the Tethys Sea in the early Tertiary. Separate *R.* (*Dipturus*)-like ancestors may have given rise to four of the five supraspecific taxa of the sister group. Absence of *R.* (*Raja*) and *R.* (*Rostroraja*) in the northern Indian Ocean suggests that they evolved after closure of the Tethys Sea. Absence of *R.* (*Okamejei*) in the eastern Atlantic likewise suggests that it evolved after closure of the Tethys Sea. The distribution of the North Pacific *Raja* assemblage suggests that it dispersed along the North Pacific rim prior to oceanic cooling which commenced in the Miocene (Hallam 1981). The amphi-American *Raja* assemblage possibly vicariated from *R.* (*Dipturus*)-like stock or *R.* (*Raja*)–*R.* (*Rostroraja*)-like stock during the widening of the Atlantic in the early Tertiary. The two eastern Pacific species of the amphi-American clade probably vicariated after emergence of the Isthmus of Panama at the end of the Pliocene (Hallam 1981). Subgroup IIa (*Cruriraja* and *Anacanthobatis*), and possibly *G.* (*Fenestraja*) of Subgroup IId, have a distributional track which may postdate the closure of the Tethys Sea or may represent the original deep-sea passage into the Atlantic from the southern Indian Ocean. The fact that these taxa occur off South Africa or in the southwestern Indian Ocean suggests that the Tethys Sea was closed before they assumed their distributional track. On the other hand, all three taxa occur along the continental slope and the shallow and narrow western Tethys Sea may have been unavailable to them.

Subgroup IIc and *Malacoraja* and *Neoraja* of Subgroup IId underwent most of their evolution within the Atlantic Ocean. Presence of species of these taxa in other oceans, i.e., North Indian Ocean, eastern Pacific, and western North Pacific is probably due to dispersal. *Raja* (*Amblyraja*), *R.* (*Leucoraja*), *R.* (*Rajella*), *Malacoraja*, and *Neoraja* are rather temperate, deep-water taxa and thus may not have been affected by closure of the Tethys Sea. Thus it is difficult to speculate on the age of these taxa. *Breviraja* and *Dacylobatus*, on the other hand, are tropical to temperate, or tropical to warm temperate in the western North Atlantic respectively. This fact suggests that they vicariated after closure of the deep-sea connection between the eastern Pacific and the western Atlantic in the Pliocene.

Gurgesiella (*Gurgesiella*) has an amphi-South American tropical to warm temperate distribution, similar to that of the amphi-American *Raja* taxon of Subgroup IIb, except that the former occurs in deeper water, does not occur in the tropical eastern North Pacific, and extends into the tropical western South Atlantic. This distributional track must date back to between the opening (Upper Paleocene) and closing (Pliocene) of the deep-sea connection between the tropical eastern Pacific and the western Atlantic.

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Appendix: Classification of Nominal Species of Skates

Group I

Raja (*Atlantoraja*)
- *Raja castelnaui*
- *Raja cyclophora*
- *Raja platana*

Raja (*Rioraja*)
- *Raja agassizi*

Bathyraja
- *Bathyraja abyssicola*
- *Bathyraja aguja*
- *Bathyraja albomaculata*
- *Bathyraja aleutica*
- *Bathyraja andriashevi*
- *Bathyraja bergi*
- *Bathyraja brachyurops*
- *Bathyraja caerulonigricans*
- *Bathyraja diplotaenia*
- *Bathyraja eatoni*
- *Bathyraja fedorovi*
- *Bathyraja griseocauda*
- *Bathyraja interrupta*
- *Bathyraja irrasa*
- *Bathyraja isotrachys*
- *Bathyraja lindbergi*
- *Bathyraja longicauda*
- *Bathyraja maccaini*
- *Bathyraja macloviana*
- *Bathyraja maculata*
- *Bathyraja magellanica*
- *Bathyraja matsubarai*
- *Bathyraja meridionalis*
- *Bathyraja minispinosa*
- *Bathyraja multispinosa*
- *Bathyraja murrayi*
- *Bathyraja notoroensis*
- *Bathyraja ogilbyi*
- *Bathyraja pallida*
- *Bathyraja papilionifera*
- *Bathyraja parmifera*
- *Bathyraja peruana*
- *Bathyraja richardsoni*
- *Bathyraja scaphiops*
- *Bathyraja schroederi*
- *Bathyraja shuntovi*
- *Bathyraja simoterus*
- *Bathyraja smirnovi*

Bathyraja (continued)
- *Bathyraja smithi*
- *Bathyraja spinicauda*
- *Bathyraja spinosissima*
- *Bathyraja trachouros*
- *Bathyraja trachura*
- *Bathyraja tzinovskii*
- *Bathyraja violacea*

Rhinoraja
- *Rhinoraja kujiensis*
- *Rhinoraja longicauda*
- *Rhinoraja odai*
- *Rhinoraja taranetzi*

Arhynchobatis
- *Arhynchobatis asperrimus*

Psammobatis
- *Psammobatis bergi*
- *Psammobatis glansdissimilis*
- *Psammobatis lentiginosa*
- *Psammobatis normani*
- *Psammobatis pavacauda*
- *Psammobatis rudis*
- *Psammobatis rutrum*
- *Psammobatis scobina*

Sympterygia
- *Sympterygia acuta*
- *Sympterygia bonapartei*
- *Sympterygia brevicaudata*
- *Sympterygia lima*

Irolita
- *Irolita waiti*

Pseudoraja
- *Pseudoraja fischeri*

Notoraja
- *Notoraja tobitukai*
- *Notoraja* sp. nov.
- *Notoraja* sp. nov.

Pavoraja
- *Pavoraja alleni*
- *Pavoraja nitida*
- *Pavoraja* sp. nov.
- *Pavoraja* sp. nov.
- *Pavoraja* sp. nov.
- *Pavoraja* sp. nov.

Subgenus A
- *Pavoraja asperula*

Subgenus A (continued)
- *Pavoraja spinifera*

Group II

Cruriraja
- *Cruriraja andamanica*
- *Cruriraja atlantis*
- *Cruriraja cadenati*
- *Cruriraja durbanesis*
- *Cruriraja parcomaculata*
- *Cruriraja poeyi*
- *Cruriraja rugosa*
- *Cruriraja triangularis*

Anacanthobatis
- *Anacanthobatis americanus*
- *Anacanthobatis borneensis*
- *Anacanthobatis donghaiensis*
- *Anacanthobatis folirostris*
- *Anacanthobatis longirostris*
- *Anacanthobatis marmoratus*
- *Anacanthobatis melanosomus*
- *Anacanthobatis nanhaiensis*
- *Anacanthobatis ori*
- *Anacanthobatis stenosomus*

Raja (*Dipturus*)
- *Raja batis*
- *Raja bullisi*
- *Raja chilensis*
- *Raja doutrei*
- *Raja floridana*
- *Raja garricki*
- *Raja gigas*
- *Raja gudgeri*
- *Raja innominata*
- *Raja johannisdavisi*
- *Raja kwangtungensis*
- *Raja laevis*
- *Raja lanceorostrata*
- *Raja leptocauda*
- *Raja lintea*
- *Raja macrocauda*
- *Raja nasuta*
- *Raja nidarosiensis*
- *Raja olseni*
- *Raja oregoni*

Raja (*Dipturus*) (continued)
- *Raja oxyrinchus*
- *Raja pullopunctata*
- *Raja springeri*
- *Raja stenorhynchus*
- *Raja teevani*
- *Raja tengu*
- *Raja trachyderma*
- *Raja whitleyi*

Raja (*Okamejei*)
- *Raja acutispina*
- *Raja australis*
- *Raja boesemani*
- *Raja cerva*
- *Raja dentata*
- *Raja heemstrai*
- *Raja hollandi*
- *Raja kenojei*
- *Raja lemprieri*
- *Raja meerdervoorti*
- *Raja polyommata*
- *Raja powelli*
- *Raja schmidti*

North Pacific *Raja* Assemblage
- *Raja binoculata*
- *Raja cortezensis*
- *Raja inornata*
- *Raja pulchra*
- *Raja rhina*
- *Raja stellulata*

Amphi-American *Raja* Assemblage
- *Raja ackleyi*
- *Raja bahamensis*
- *Raja cervigoni*
- *Raja eglanteria*
- *Raja equatorialis*
- *Raja texana*
- *Raja velezi*

Raja (*Raja*)
- *Raja africana*
- *Raja asterias*
- *Raja brachyura*
- *Raja clavata*
- *Raja herwigi*
- *Raja maderensis*

Group II (continued)

- *Raja* (*Raja*) (continued)
  - *Raja microocellata*
  - *Raja miraletus*
  - *Raja montagui*
  - *Raja polystigma*
  - *Raja radula*
  - *Raja rouxi*
  - *Raja straeleni*
  - *Raja undulata*
- *Raja* (*Rostroraja*)
  - *Raja alba*
- *Raja* (*Amblyraja*)
  - *Raja badia*
  - *Raja doellojuradoi*
  - *Raja frerichsi*
  - *Raja georgiana*
  - *Raja hyperborea*
  - *Raja jenseni*
  - *Raja radiata*
  - *Raja reversa*
  - *Raja robertsi*
- *Raja* (*Rajella*)
  - *Raja annandalei*
  - *Raja bathyphila*
  - *Raja bigelowi*
  - *Raja caudispinosa*
  - *Raja confundens*
  - *Raja dissimilis*
  - *Raja fuliginea*
  - *Raja fyllae*
  - *Raja kukujevi*
  - *Raja leopardus*
  - *Raja nigerrima*
  - *Raja purpuriventralis*
  - *Raja ravidula*
  - *Raja sadowskyi*
- *Raja* (*Leucoraja*)
  - *Raja circularis*
  - *Raja erinacea*
  - *Raja fullonica*
  - *Raja garmani*
  - *Raja leucosticta*
- *Raja* (*Leucoraja*) (continued)
  - *Raja melitensis*
  - *Raja naevis*
  - *Raja ocellata*
  - *Raja wallacei*
  - *Raja yucatanensis*
- *Dactylobatus*
  - *Dactylobatus armatus*
  - *Dactylobatus clarki*
- *Breviraja*
  - *Breviraja claramaculata*
  - *Breviraja colesi*
  - *Breviraja marklei*
  - *Breviraja nigriventralis*
  - *Breviraja schroederi*
  - *Breviraja spinosa*
- *Malacoraja*
  - *Malacoraja kreffti*
  - *Malacoraja senta*
  - *Malacoraja spinacidermis*
- *Neoraja*
  - *Neoraja africana*
  - *Neoraja caerulea*
  - *Neoraja carolinensis*
  - *Neoraja stehmanni*
- *Gurgesiella* (*Fenestraja*)
  - *Gurgesiella atripinna*
  - *Gurgesiella cubensis*
  - *Gurgesiella ishiyamai*
  - *Gurgesiella mamillidens*
  - *Gurgesiella plutonia*
  - *Gurgesiella sibogae*
  - *Gurgesiella sinusmexicanus*
  - *Gurgesiella* sp. nov.
- *Gurgesiella* (*Gurgesiella*)
  - *Gurgesiella atlantica*
  - *Gurgesiella dorsalifera*
  - *Gurgesiella furvescens*
- *Incertae sedis*
  - *Raja rondeleti*

Taxonomy of the Genus *Dasyatis* (Elasmobranchii, Dasyatididae) from the North Pacific

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ABSTRACT

Species of the genus *Dasyatis* Rafinesque, 1810 from the North Pacific were taxonomically reviewed. Nineteen species were recognized as valid, including two unnamed species from Taiwan. They were divided into five groups based on the shape of their disc and the presence or absence of a dorsal tail fold or keel. Some characters (e.g., number of oral papillae, tail length) were found to have wide variation, but some new characters were also found to be useful (e.g., a pair of large teeth on the upper jaw in *D. kuhlii*, an anteriorly curved groove on the ventral side of the disc in *D. matsubarai*). *Urolophoides* Lindberg, 1930 was considered as a junior synonym of *Dasyatis*. A key to the 19 species of *Dasyatis* from the North Pacific is presented.

Introduction

Dasyatis is the largest genus of the family Dasyatididae. Since Rafinesque's (1810) description of the genus *Dasyatis*, many systematic works have been done (Garman 1913; Beebe and Tee-Van 1941; Fowler 1941; Bigelow and Schroeder 1953; Matsubara 1955; Chu 1960; Teng 1962; Wallace 1967; Misra 1969; Chen and Chung 1971; Compagno and Heemstra 1984; Compagno and Roberts 1984; Shen 1984; Monkolprasit 1984; Chu and Meng 1987). However, taxonomic works on the North Pacific *Dasyatis* are limited to local waters, and no comprehensive study has ever been made. In addition, past studies have employed taxonomic characters which sometimes vary individually, sexually and ontogenetically, and these often cause confusion. Therefore, a revision of the North Pacific *Dasyatis* is necessary.

Materials and Methods

Institutional acronyms follow Leviton et al. (1985). Methods and terminology of counts and measurements follow Nishida and Nakaya (1988a). Number of oral papillae is expressed by the following formula: number of papillae on the left corner—number in the center—number on the right corner (e.g., 0-3-0, 2-3-2 in Table 1). Proportional measurements of the body are presented in percentage of disc width (DW).

Genus *Dasyatis* Rafinesque, 1810

Dasyatis Rafinesque, 1810: 16 (type species *Dasyatis ujo* Rafinesque).

Description—Disc trapezoidal, rhomboid or rhomboid with extremely elongate snout. Tail whip-like and usually longer than disc, with a serrated tail spine (or spines). Ventral tail fold not extending to tip of tail, and with or without dorsal tail fold or keel.

Remarks—*Urolophoides* was described by Lindberg in Soldatov and Lindberg (1930) for their *U. giganteus*, based on a stuffed specimen. This genus differs from *Dasyatis* in having a short, stout, and non-whiplike tail. Bigelow and Schroeder (1953) considered it a doubtful genus, but some authors (Lindberg and Legeza 1959; Compagno and Roberts 1984) recognize the genus. However, tails of stingrays are easily damaged and sometimes it is even difficult to determine whether or not the tail has been damaged. In addition, specimens with a short tail like that of *Urolophoides* are often seen among other species of *Dasyatis* (Bigelow and Schroeder 1953; *D. kuhlii*, *D. matsubarai*, and *D. izuensis* in this study). Other diagnostic characters of *Urolophoides*

Table 1.
Variations in number of oral papillae. Number of specimens which show each pattern are given.

Pattern of oral papillae	*D. akejei* $n = 23$	*D. matsubarai* $n = 23$	*D. violacea* $n = 5$
0-0-0	0	2	1
0-3-0	1	0	0
0-3-1	1	0	0
0-4-0	0	1	0
1-3-1	14	2	0
1-4-0	0	1	0
2-3-0	2	0	0
1-3-2	2	1	0
1-4-1	0	2	0
2-3-1	1	3	0
1-5-1	0	2	0
2-3-2	2	0	0
2-4-1	0	2	0
2-5-1	0	1	0
3-3-2	0	1	0
3-4-1	0	1	0
3-3-3	0	1	0
3-4-3	0	1	0
3-4-5	0	1	0
3-7-2	0	1	0
0-13-0	0	0	1
0-14-0	0	0	1
0-15-0	0	0	2

do not separate it from *Dasyatis*. Thus we could not find any generic differences between them, so we regard *Urolophoides* as a junior synonym of *Dasyatis*.

Key to the Species of *Dasyatis* from the North Pacific

1a. Disc trapezoidal (Fig. 1A); ventral surface of disc uniformly dark purple .... ***D. violacea*** **(Bonaparte, 1832)**

1b. Disc rhomboid (Fig. 1B,C); ventral surface of disc pale 2

2a. Disc rhomboid with extremely elongate snout (Fig. 1B); anterior margin of disc broadly concave 3

2b. Disc rhomboid with moderate to short snout (Fig. 1C); anterior margin of disc convex, straight, or concave 4

3a. Dorsal tail fold or keel usually absent; eyeball 1/10–1/15 of preorbital snout length; ventral tail fold length about 1/5 of DW; total pectoral radials 129–135, pelvic radials 23–25 in male and 26–28 in female, prespine separate centra 121–139, intestinal valve turns 22–24; matures larger than 300 mm DW .... ***D. acutirostra*** **Nishida and Nakaya, 1988**

3b. Dorsal tail fold present; eyeball 1/3–1/8 of preorbital snout length; ventral tail fold length about 2/3 of DW; total pectoral radials 106–114, pelvic radials 17–19 in male and 20–23 in female, prespine separate centra 95–100, intestinal valve turns 16–18; matures between 200–300 mm DW .... ***D. zugei*** **(Müller and Henle, 1841)**

4a. Dorsal tail fold or keel absent 5

4b. Dorsal tail fold or keel present 8

5a. Ventral tail fold height 2 to 3 times deep as tail; dorsal surface of disc thickly covered with small denticles in adult; eyeball diameter about 1/3 of interorbital width..... ***D. sephen*** **(Forsskål, 1775)**

5b. Ventral tail fold height less than tail depth; margin of disc smooth even in adult; eyeball diameter about half of interorbital width 6

6a. Tail length about 3 times disc length; disc longer than 90% of DW; snout longer than 25% of DW; head length about half of DW; prespine length longer than 120% of DW .... ***D. bennetti*** **(Müller and Henle, 1841)**

6b. Tail length about twice disc length; disc about 80% of DW; snout shorter than 20% of DW; head length shorter than half of DW; prespine length shorter than 110% of DW 7

7a. Anterior margin of disc nearly straight; prespine length about 110% of DW; dorsal surface of disc with a row of large midline tubercles in a specimen of 520.7 mm DW; ventral surface of disc white .... ***D. latus*** **(Garman, 1880)**

7b. Anterior margin of disc undulate; prespine length about 100% of DW; dorsal surface of disc smooth in a specimen of 530.1 mm DW; ventral surface of disc white with dark gray margin .... ***D.*** **sp. 1**

8a. Dorsal surface of disc with many small bluish spots; tail with white and black bands; a pair of large teeth present on upper jaw (Fig. 9); intestinal valve turns 14–15; snout shorter than 1/6 of DW .... ***D. kuhlii*** **(Müller and Henle, 1841)**

8b. Dorsal surface of disc without bluish spots; tail without bands; large teeth absent; intestinal valve turns usually more than 18; snout longer than 1/6 of DW 9

9a. Head length about 1/4 of DW; eyeball about 1/7 of interorbital width; disc shorter than 80% of DW; total length about 130% of DW .... ***D. giganteus*** **(Lindberg, 1930)**

9b. Head length longer than 1/3 of DW; eyeball 1/3 or less of interorbital width; disc longer than 80% of DW; total length longer than 130% of DW 10

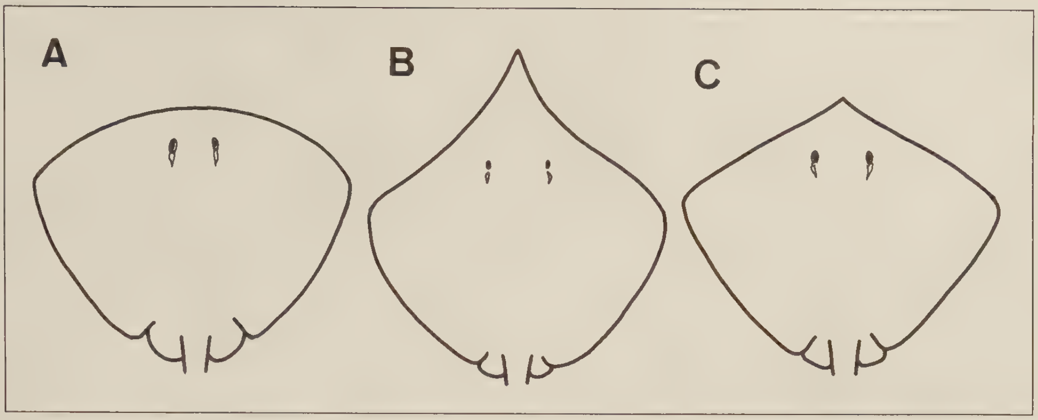

Figure 1.
Disc shape in species of *Dasyatis*. A, trapezoidal; B, rhomboid with extremely elongate snout; C, rhomboid.

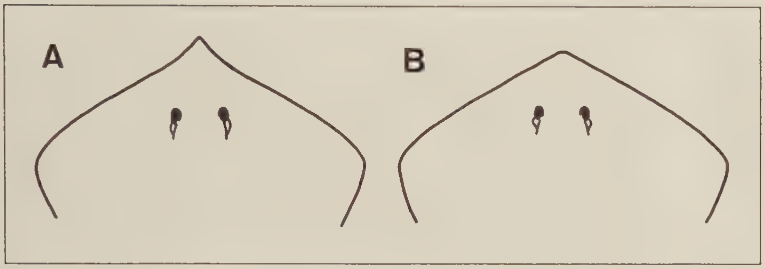

Figure 2.
Snout tip of *Dasyatis* with rhomboid disc. A, triangular and produced; B, blunt and not produced.

10a. Dorsal surface of disc with many white spots; an anteriorly curved groove present on ventral side just behind pectoral girdle (see Fig. 19); total pectoral radials 120–124, intestinal valve turns 25-26 .... ***D. matsubarai*** **Miyosi, 1939**

10b. Dorsal surface of disc without white spots; an anteriorly curved groove absent; total pectoral radials usually less than 120, intestinal valve turns usually less than 22 .... **11**

11a. Ventral tail fold white, its length shorter than 1/3 of disc length; tail length about same as DW .... ***D. izuensis*** **Nishida and Nakaya, 1988**

11b. Ventral tail fold black or dark colored, its length longer than 1/3 of disc length; tail length longer than DW **12**

12a. Disc length shorter than 85% of DW; dorsal surface of disc entirely smooth even in adult .... ***D. laevigatus*** **Chu, 1960**

12b. Disc length longer than 85% of DW; dorsal surface of disc more or less rough with tubercles or denticles **13**

13a. Snout triangular and produced (Fig. 2A) **14**

13b. Snout blunt and not produced (Fig. 2B) **17**

14a. Dorsal surface of disc and prespine region with a band of small middorsal denticles ... . ***D. sinensis*** **(Steindachner, 1892)**

14b. Dorsal surface of disc and prespine region with a row of midline tubercles **15**

15a. Dorsal surface of disc brown; ventral surface white with yellowish brown margin and irregular spots; upper side of eyeball and spiracle with orangish or yellowish margins; prespine length shorter than 125% of DW .... ***D. akajei*** **(Müller and Henle, 1841)**

15b. Dorsal surface of disc uniformly chocolate brown; ventral surface pale without yellowish brown margin and spots; upper side of eyeball and spiracle without margins; prespine length longer than 125% of DW **16**

16a. Precloacal length 92.1% of DW; ventral tail fold length 50.0% of DW .... ***D. navarrae*** **(Steindachner, 1892)**

16b. Precloacal length 81.2% of DW; ventral tail fold length 64.6% of DW............. ***D.*** **sp. 2**

17a. Ventral tail fold short (33.3% of DW) and high .... ***D. brevis*** **(Garman, 1880)**

17b. Ventral tail fold relatively long (42.2% of DW in *D. ushiei*) and low **18**

18a. Disc length 89% of DW; prespine length 117.6% of DW; disc with a row of midline tubercles in specimens of 284.5 and 350.5 mm DW .... ***D. longus*** **(Garman, 1880)**

18b. Disc length 81.6% of DW; prespine length 107.6% of DW; disc smooth in a specimen of 367 mm DW .... ***D. ushiei*** **Jordan and Hubbs, 1925**

Taxonomy of North Pacific Species of *Dasyatis*

Dasyatis sephen (Forsskål, 1775) (Fig. 3, Table 2)

Raja sephen Forsskål, 1775: VIII, 17 (Djedda and Lohaja, Red Sea).
Trigon forskalii Rüppell, 1828: 53, pl. 13, fig. 2.
Trigon sephen. Rüppell, 1828: 52.
Trygon sephen. Günther, 1870: 482.
Hypolophus sephen. Müller and Henle, 1841: 170.
Dasyatis sephen. Fowler, 1929: 505.
Pastinachus sephen. Marshall, 1964: 39, pl. 14, fig. 45.
Dasyatis bennetti (not of Müller and Henle). Masuda et al. 1975: 161, pl. 12-C.
Dasyatis (*Pastinachus*) *sephen*. Monkolprasit, 1984: 113, fig. 58.

Material Examined—HUMZ 97223, 708.5 mm DW, female, Haneji Bay, Okinawa Pref., Japan; HUMZ 101448, 519.0 mm DW, male, Nago Fish Market, Okinawa Pref., Japan; MTUF 20643, 407.2 mm DW, male, 29°07′N, 48°40′E, Arabian Gulf; MTUF 25108, 402.2 mm DW, male, data unknown.

Description—Disc rhomboid, anterior margin nearly straight and posterior margin convex. Disc wide, precloacal length about 2/3 of DW, disc length about 4/5 of DW. Dorsal surface of disc smooth in young, but thickly covered by small denticles with two to four midline tubercles in adults. Eye small, eyeball diameter about 1/3 of interorbital width, and 1/6 of snout. Upper jaw heavily undulated. Tail spine inserted on first third of tail. Ventral tail fold very high and long (about 90% of DW), but falling short of tip of tail. Dorsal tail fold or keel absent. Intestinal valve turns 20–22.

Dorsal surface of disc grayish brown and ventral surface whitish. Ventral tail fold grayish brown.

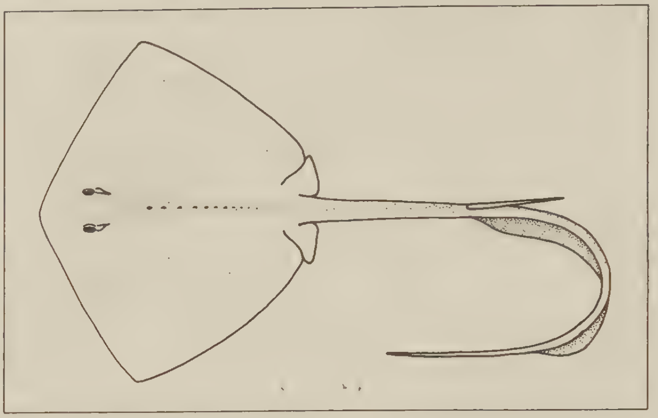

Figure 3.
Dasyatis sephen, 708.5 mm DW, female, HUMZ 97223.

Table 2.
Proportional measurement (as % of DW) and counts of the North Pacific *Dasyatis*. Number and sex of specimens are given in parentheses.

	D. sephen 402.0–708.5[a] (3M, 1F)	*D. violacea* 425.8–578.4 (6M, 2F)	*D. akajei* 119.2–407.6 (8M, 15F)	*D. bennetti* 191.3, 325.7 (1M, 1F)	*D. kuhlii* 221.3–435.8 (4M, 3F)	*D. zugei* 106.6–291.0 (7M, 5F)
Proportional measurements						
Total length	217.6–247.6	152.6–187.5	194.5–235.4	370.3, 374.0	143.9–196.0	209.7–286.2
Disc length	78.2–79.5	74.1–75.7	87.0–92.1	92.2, 95.9	80.4–83.5	94.6–104.9
Precloacal length	65.5–68.8	61.6–64.6	73.0–78.8		67.0–69.7	81.8–95.2
Head length	33.0–38.0	32.3–36.5	42.0–46.9	48.0, 50.2	36.5–38.9	48.5–59.5
Preorbital snout length	13.1–18.0	10.0–12.5	17.4–21.9	25.7, 27.4	12.7–15.4	24.6–33.8
Eyeball diameter	3.2–4.6	4.9–5.8	4.7–5.4	4.4, 5.4	6.1–6.4	4.1–6.6
Interorbital width	7.9–11.5	8.6–10.7	10.3–11.5	10.6, 10.9	6.7–8.3	8.1–10.9
Prespine length	127.0	94.9–100.9	107.6–122.1	120.6, 130.5	102.6–105.4	119.6–134.6
Ventral tail fold length	87.4	21.0–25.6	36.2–48.6	60.2, 67.4	70.5–71.3	71.5–90.7
Counts						
Oral papillae	5	0–15	3–7	3, 5	2	0
Upper jaw teeth	31	31–39	29–39	31	24–29	40–55
Lower jaw teeth	19	33–37	33–47	33	34–36	39–55
Intestinal valve turns	20–22	18–21	18–21	22	14–15	16–18
Prespine separate centra		94–99	103–114	119	99–111	95–100
Total pectoral radials		94–100	98–112	122, 123	103–113	106–114
Pelvic radials in male		14	20–23	21	18–19	17–19
Pelvic radials in female		19	26–28	24	24	20–23

Table 2. (continued)

	D. brevis 225.1[a] (1M)	*D. latus* 520.7 (1F) original description	*D. longus* 284.5, 350.5 (1?, 1F) original description	*D. navarrae* 316.0 (1M)	*D. sinensis* 380.0 (1M)	*D. ushiei* 367.0 (1M)	*D. giganteus* 1780.0 (1F) original description
Proportional measurements							
Total length	207.4	250.2	286.2, 301.8		223.2	267.8	130.3
Disc length	88.9	79.6	89.0	94.9	95.5	81.6	78.7
Precloacal length	78.4			92.1	82.4	71.1	
Head length	42.2			52.8	45.5	41.7	27.5
Preorbital snout length	15.9	16.1	18.7	25.4	24.9	16.9	20.2
Eyeball diameter	6.7	5.4	5.5	4.4	4.9	5.7	1.7
Interorbital width	9.8	11.8	11.0	14.2	12.4	10.4	13.5
Prespine length	112.7	109.8	117.6	128.8		107.6	
Ventral tail fold length	33.3			50.0	45.0	42.2	
Counts							
Oral papillae	5	5-6	5	3	5	7	
Upper jaw teeth	36			40	37	42	
Lower jaw teeth	38			37	40	45	
Intestinal valve turns	22					26	
Prespine separate centra	124					124	
Total pectoral radials	120				106	128	
Pelvic radials in male	24				23	20	
Pelvic radials in female							

	D. matsubarai 324.8-1830.0[a] (12M, 12F)	*D. laevigatus* (1M, 1F) original description	*D. acutirostra* 281.4-724.8 (11M, 10F)	*D. izuensis* 182.6-418.2 (5M, 3F)	*D.* sp. 1 530.1 (1F)	*D.* sp. 2 437.2 (1M)
Proportional measurements						
Total length	132.2-193.1		234.1-296.2	158.0-187.3	238.9	301.2
Disc length	81.7-88.7	76.9, 83.3	99.1-106.1	86.4-91.8	80.9	94.2
Precloacal length	68.2-75.2		86.1-95.3	73.6-79.1	67.4	81.2
Head length	38.9-43.6		56.8-63.0	37.7-43.4	38.3	45.8
Preorbital snout length	16.8-22.0	17.1, 18.5	36.9-43.9	14.1-18.7	16.7	19.4
Eyeball diameter	3.2-5.7	5.7, 6.2	2.4-3.8	4.8-7.1	4.4	4.4
Interorbital width	9.7-12.8	8.6, 9.3	8.5-9.8	9.7-12.0	9.1	10.6
Prespine length	105.2-117.5		116.8-128.5	111.2-118.2	101.4	127.3
Ventral tail fold length	31.0-44.0	49.2, 53.3	15.0-22.9	24.6-32.3	42.4	64.6
Counts						
Oral papillae	0-12	3	0	5	7	5
Upper jaw teeth	34-44	40	40-51	27-41	39	51
Lower jaw teeth	33-46		39-49	31-39	45	49
Intestinal valve turns	25-26		22-24	18-20	26	19
Prespine separate centra	113-129		121-139	101-110	116	113
Total pectoral radials	120-124		129-135	102-105	129	109
Pelvic radials in male	18-20		23-25	20-21		19
Pelvic radials in female	26		16-28	26-27	28	

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[a] Disc width in mm.

Distribution—Okinawa, Japan; Indonesia; Melanesia; Australia in the eastern Indian Ocean and western Pacific Ocean; South Africa in the western Indian Ocean; and Red Sea. Reported also from fresh and brackish waters.

Remarks—Whether *sephen* should be placed in the genus *Dasyatis* or *Hypolophus* Müller and Henle, 1841 is currently under investigation. Among some recent works, Grant (1982), Nakaya (1984), Sainsbury et al. (1985), and Kuronuma and Abe (1986) place it in *Dasyatis*; while Compagno and Roberts (1982, 1984), Gloerfelt-Tarp and Kailola (1984), and Compagno (1986) place it in *Hypolophus*.

However, based on the phylogenetic study, the senior author considers that *Hypolophus* is a synonym of *Dasyatis* (unpubl. data). Therefore we place *sephen* in *Dasyatis*.

Dasyatis violacea (Bonaparte, 1832) (Figs. 4, 5, Table 2)

Trygon violacea Bonaparte, 1832: fasc. I.
Pteroplatytrygon violaceum. Fowler, 1910: 474.
Dasybatus violaceus. Garman, 1913: 390.
Dasyatis violacea. Bigelow and Schroeder, 1953: 343.
Dasyatis atratus Ishiyama and Okada, 1955: 95, figs. 1, 2.
Dasyatis guileri Last, 1979: 172, fig. 1.

Material Examined—HUMZ 6238, 503.0 mm DW, male, Indian Ocean; HUMZ 75873, 464.2 mm DW, male, 13°46′S, 174°15′E, near Vanuatu, Pacific Ocean; HUMZ 106471, 578.4 mm DW, female, Odawara Fish Market, Kanagawa Pref., Japan; HUMZ 107600, 107601, 444.8, 462.4 mm DW, 2 males, data unknown; HUMZ 111741, 500.6 mm DW, male, data unknown; HUMZ 111742, 425.8 mm DW, male, data unknown; HUMZ 111749, 383.0 mm DW, female, data unknown.

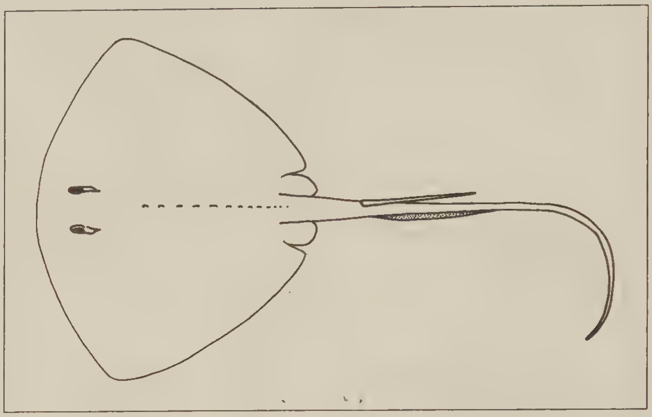

Figure 4.
Dasyatis violacea, 578.4 mm DW, female, HUMZ 106471.

Description—Disc trapezoidal, anterior margin convex and posterior margin nearly straight. Outer corner of disc angular. Disc short, its length about 3/4 (74.1–75.7%) of DW. Snout short and rounded, its length only 10.0–12.5% of DW. Teeth with a cusp in adult male and even in adult female (Fig. 5). Oral papillae 0-0-0 to 0-15-0 (Table 1). Dorsal surface of disc smooth in young, but middorsal area covered by small denticles, and disc with a row of midline tubercles in adults. Prespine length short, about the same as DW (94.9–100.9% of DW). Dorsal tail fold or keel absent, but ventral tail fold present. Ventral tail fold short, its length shorter than 1/4 of DW. Prespine separate centra 94–99, total pectoral radials 94–100, and pelvic radials 14 in male and 19 in female.

Dorsal and ventral surface of disc, and ventral tail fold dark purple.

Distribution—Cosmopolitan in tropical to temperate seas, reported from the Atlantic and eastern Pacific Oceans, Mediterranean, southern Africa, South China Sea, southern Japan, Tasmania, and west Africa. *Dasyatis violacea*, a pelagic species, is occasionally caught on tuna longline (Ishiyama and Okada 1955).

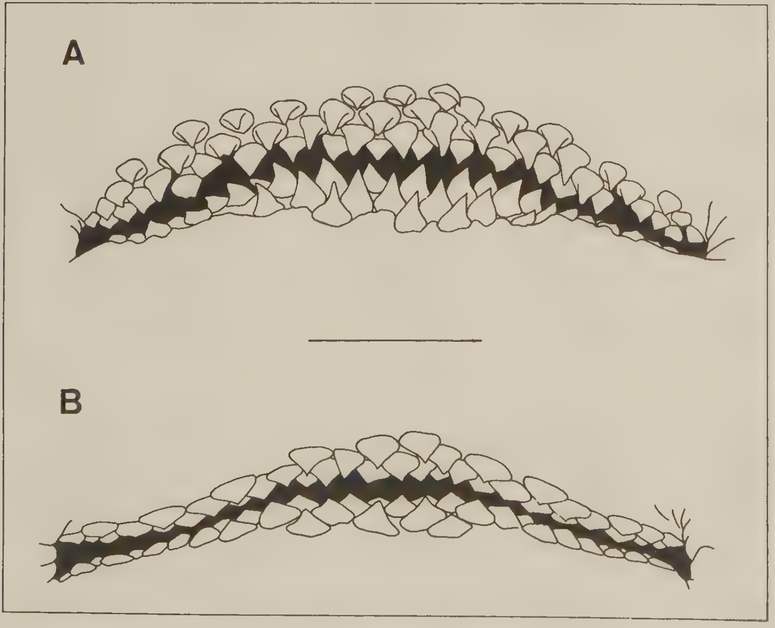

Figure 5.
Upper and lower jaw teeth of *Dasyatis violacea*. A, male; B, female. Scale bar = 10 mm.

Dasyatis akajei (Müller and Henle, 1841) (Fig. 6, Table 2)

Trygon akajei Müller and Henle, 1841: 165, pl. 54, fig. 1 (southwest coast of Japan).
Dasyatis akajei. Jordan and Fowler, 1903: 659, fig. 9.

Material Examined—RMNH 4255a, lectotype, 146.4 mm DW, female, southwest coast of Japan; RMNH 4255b, paralectotype, 122.0 mm DW, male, southwest coast of Japan; HUMZ 105439, 189.1 mm DW, female, Minamikayabe, Hokkaido Pref., Japan; HUMZ 105908, 241.0 mm DW, male, off Itado, Shizuoka Pref., Japan; HUMZ 105945, 224.2 mm DW, female, off Shimoda, Shizuoka Pref., Japan; HUMZ 105970, 162.7 mm DW, female, off Shimoda, Shizuoka Pref., Japan; HUMZ 107042, 142.3 mm DW, female, off Kunousan, Shizuoka Pref., Japan; HUMZ 107451, 226.2 mm DW, female, off Shimoda, Shizuoka Pref., Japan; HUMZ 109714, 140.0 mm DW, female, Japan; HUMZ 109734-109738, 193.8–407.6 mm DW, 4 males and a female, Japan; HUMZ 109740, 277.6 mm DW, female, Japan; HUMZ 110562-110568, 119.2–187.9 mm DW, 2 males and 5 females, off Kashiwazaki, Niigata Pref., Japan; FAKU W296, 188.6 mm DW, female, Nishi-Maizuru Fish Market, Kyoto Pref., Japan.

Description—Disc rhomboid, anterior margin nearly straight and posterior margin convex. Snout triangular and slightly produced. Oral papillae 0-3-0 to 2-3-2. Dorsal surface of disc smooth in young, but interorbital, middorsal, and shoulder regions covered with small denticles. Disc with a row of midline tubercles in adult. Tail moderate in length, its length longer than DW, but shorter than 1.5 times DW. In adults, tail with one to six prespine tubercles, and rough with asperities distally.

Dorsal surface of disc brown, upper side of eyeball and spiracle with orangish or yellowish margins. Ventral surface of disc and pelvic fin white with yellowish brown margin and yellowish spots of irregular form and disposition. Anterior part of ventral side of tail with yellowish irregular spots, lateral side of tail yellowish, ventral tail fold blackish.

Distribution—Commonly found in Japanese waters, and also reported from Korea, Taiwan and China.

Remarks—Boeseman (1947) examined all syntypes of *D. akajei* in detail and designated RMNH 4255a as the lectotype. We also examined the lectotype and one of the paralectotypes (RMNH 4255b). The number of oral papillae, which lie on the mouth floor, is often used as a diagnostic taxonomic character within this genus. However, nothing is known about variation in papillae number. Müller and Henle (1841) and Boeseman (1947) counted only three oral papillae in the syntypes. We also examined the number of oral papillae in the type specimens and found three large papillae at the symphysis and two small papillae on the left corner of mouth in the lectotype. The right corner of its mouth was damaged and oral papillae could not be counted. However, the paralectotype has three large papillae at the symphysis, and no papillae at the corners of the mouth. We made counts of the oral papillae in the other specimens of *D. akajei*, and found wide variation (Table 1). We also examined specimens of the other species. *D. violacea* was found to have 0 to 15 oral papillae, and *D. matsubarai* 0 to 12 papillae (Table 1). However, *D. kuhlii* always has two large distinct papillae, and *D. zugei* and *D. acutirostra* lack the oral papillae on the mouth floor. These data show that a degree of variation in the number of oral papillae exists in species of *Dasyatis*. The number of oral papillae can not be reliably used as a taxonomic character in some species.

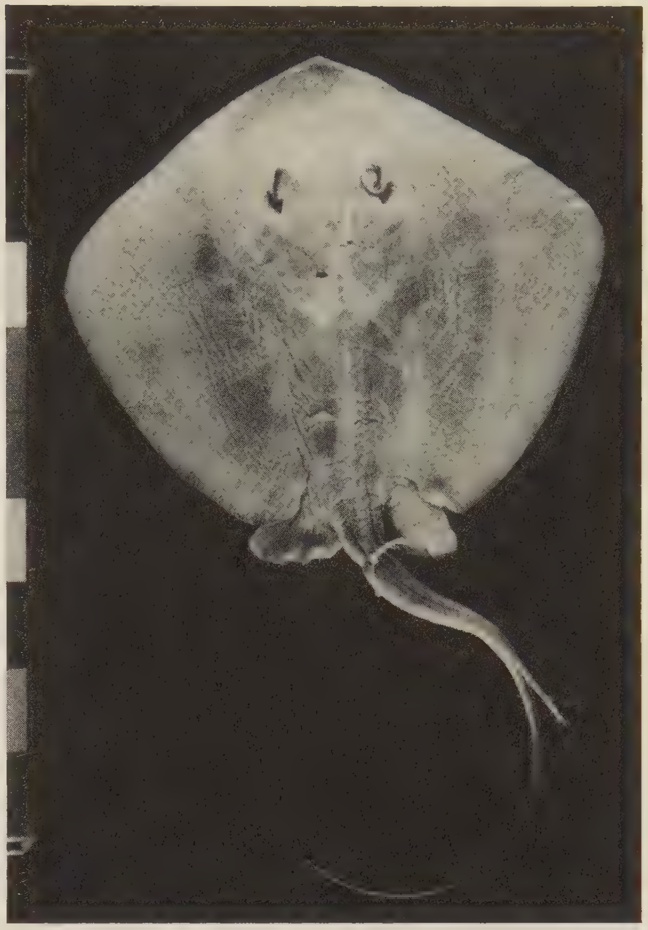

Figure 6.
Dasyatis akajei, lectotype, 146.4 mm DW, female, RMNH 4255a.

Dasyatis bennetti (Müller and Henle, 1841) (Fig. 7, Table 2)

Trygon bennetti Müller and Henle, 1841: 160, pl. 52 (China and Trinidad).
Trygon bennettii. Günther, 1870: 480.
Dasybatus bennetti. Garman, 1913: 383.
Dasyatis bennettii. Fowler, 1929: 505.
Dasyatis bennetti. Chen, 1948: 29, 44.
Dasyatis zugei (not of Müller and Henle). Faculty of Fisheries, University of Nagasaki, 1973: 399, pl. 19.

Material Examined—HUMZ 101469, 191.3 mm DW, female, data unknown; HUMZ 101477, 325.7 mm DW, male, data unknown.

Description—Disc rhomboid, anterior margin straight, and posterior margin convex. Snout angular and moderately produced. Head length about half (48.0–50.2%) of DW, and snout about 1/4 (25.7–27.4%) of DW. Dorsal surface of disc smooth in young except for small denticles in mid-dorsal area. Adults with a row of midline tubercles. Tail very long, its length about 3 times disc length, and rough posteriorly with small asperities. Dorsal tail fold or keel absent, but ventral tail fold present. Ventral tail fold longer than half (60.2–67.4%) of DW. Prespine separate centra 119, pectoral radials 122, 123, pelvic radials 21 in male and 24 in female, and intestinal valve turns 22.

Dorsal surface of disc yellowish brown and ventral surface whitish. Ventral tail fold dark colored.

Distribution—*Dasyatis bennetti* is widely reported from the Indian, Pacific, and Atlantic Oceans. However, some records seem to be based on misidentification.

Dasyatis kuhlii (Müller and Henle, 1841) (Figs. 8, 9, Table 2)

Trygon kuhlii Müller and Henle, 1841: 164, pl. 50 (Vanicolo Is., New Guinea, India).
Dasyatis kuhlii. Jordan and Fowler, 1903: 659.
Dasybatus kuhlii. Garman, 1913: 395.
Dasyatis (*Amphotistius*) *kuhlii*. Misra, 1969: 150, text-fig. 48.

Material Examined—HUMZ 37684, 272.4 mm DW, male, off Sarawak, Borneo; HUMZ 103527, 435.8 mm DW, female, Izu-oshima, Tokyo Pref., Japan; HUMZ 105502, 105503, 221.3, 309.8 mm DW, 1 male and 1 female, off Kochi, Kochi Pref., Japan; HUMZ 111226, 374.1 mm DW, male, off Kuroshima, Okinawa Pref., Japan; HUMZ111228, 408.4 mm DW, male, off Kuroshima, Okinawa Pref., Japan; HUMZ 111743, 296.6 mm DW, female, Japan.

Description—Disc rhomboid and thick, anterior and posterior margins slightly convex. Outer and posterior corners of disc angular. Snout not produced, its length rather short (12.7–15.4% of DW). Eyeball large, its diameter slightly less than interorbital width (6.1–6.4% of DW). A pair of large teeth present on upper jaw (Fig. 9). Two oral papillae. Dorsal surface of disc smooth in young, but with a row of midline tubercles in adults. Distinctive dorsal tail keel and ventral tail fold present, and supported by reduced radials. Ventral tail fold length nearly 3/4 (70.5–71.3%) of DW. Very few intestinal valve turns (14–15).

Ground color of dorsal surface of disc pale brown; two dark brown transverse bands present on interorbital region; numerous irregularly distributed small blue spots, each with a dark colored margin. Ventral surface of disc whitish. Tail darker distally, with some white and black bands. Ventral tail fold blackish.

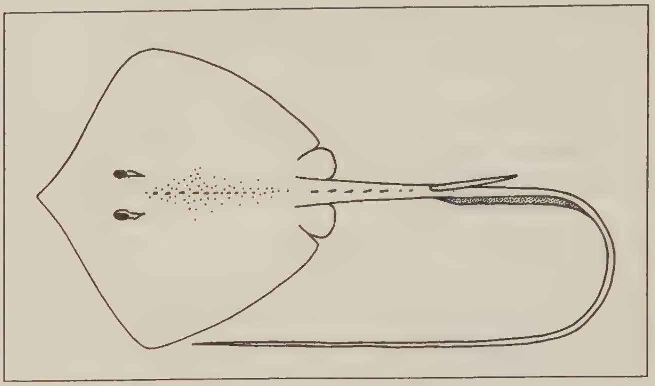

Figure 7.
Dasyatis bennetti, 191.3 mm DW, female, HUMZ 101469.

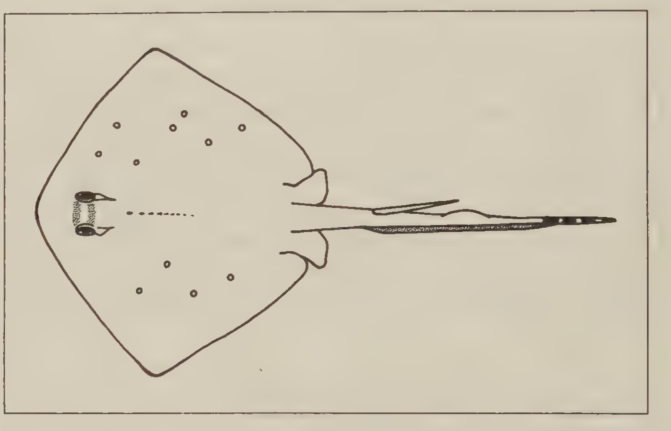

Figure 8.
Dasyatis kuhlii, 296.6 mm DW, female, HUMZ 111743.

Distribution—Widely distributed from Indian Ocean to Japan and Australia.

Remarks—This species is characterized by its bluish spots on the dorsal side of the disc, and white and black ring-like bands on the distal part of tail. These spots and bands

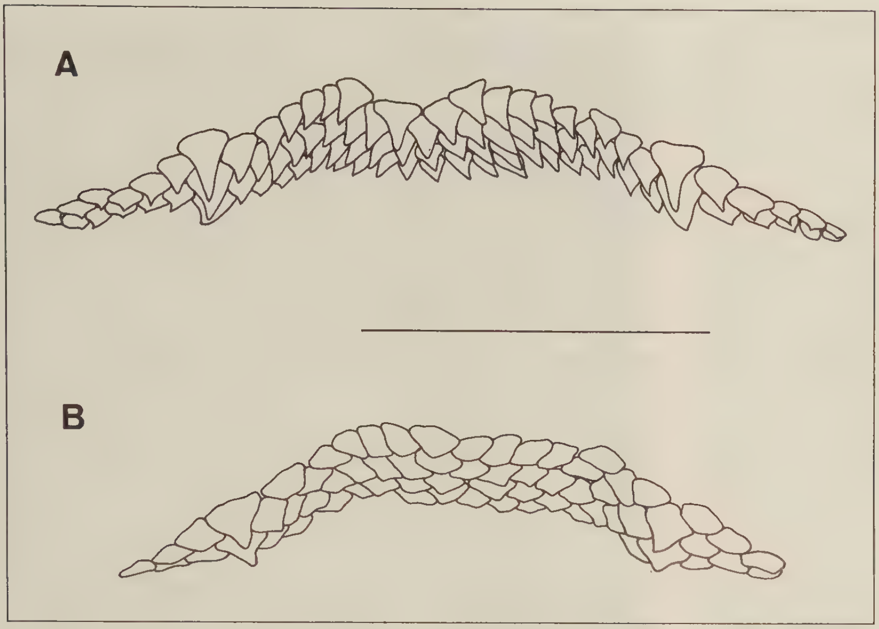

Figure 9.
Upper jaw teeth of *Dasyatis kuhlii*. A, male; B, female. Scale bar = 10 mm.

are often faint in large specimens, but this species can be clearly differentiated from other species in having a short snout (12.7–15.4% of DW), a large eyeball slightly less than interorbital width, a pair of large teeth on upper jaw (Fig. 9), a long ventral tail fold nearly 3/4 of DW, and very few intestinal valve turns (14–15).

Dasyatis zugei (Müller and Henle, 1841) (Fig. 10, Table 2)

Trygon zugei Müller and Henle, 1841: 165, pl. 55 (China, India, Japan).
Trygon crozieri Blyth, 1860: 45.
Dasyatis zugei. Jordan and Fowler, 1903: 660 (in part).
Dasybatus zugei. Garman, 1913: 398 (in part).
Dasyatis cheni Teng, 1962: 237, fig. 65.
Dasyatis (*Amphotistius*) *zugei*. Misra, 1969: 152, text-fig. 49.

Material Examined—MNHN 1987-152, lectotype, 137.0 mm DW, male, Macao, China; MNHN A 7934, paralectotypes 182.5–208.0 mm DW, male and female, Pondicherry, India; MNHN 2447, paralectotype, 106.6 mm DW, male, Macao, China; RMNH D 2447, paralectotype, 228mm DW, female, Japan; RMNH D 2448, paralectotype, 180 mm DW, male, Japan; TFRI 2776, holotype of *Dasyatis cheni*, 291 mm DW, female, Keelung, Taiwan; USNM 75870, 228.9 mm DW, male, Japan?; USNM 75872, 127 mm DW, female, Japan; HUMZ 105941, 238.0 mm DW, male, Yawatahama, Ehime Pref., Japan; HUMZ 107599, 168.7 mm DW, male, Yawatahama, Ehime Pref., Japan; MTUF 25124, 170.0 mm DW, female, off Mogi, Nagasaki Pref., Japan.

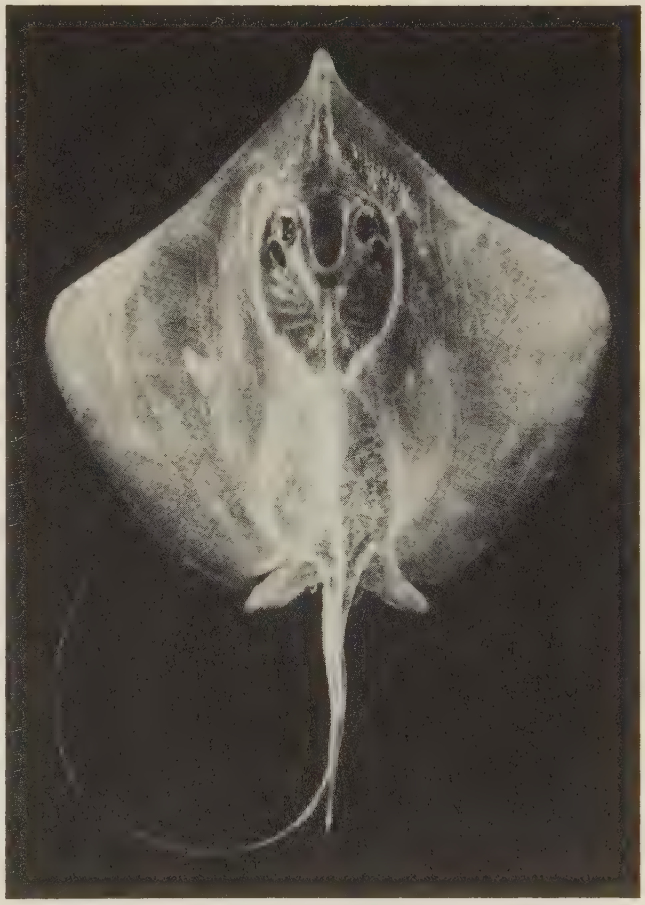

Figure 10.
Dasyatis zugei, lectotype, 137.0 mm DW, male, MNHN 1987-152.

Description—Disc rhomboid with extremely elongate snout, anterior margin concave and posterior margin convex. Preorbital snout length 1/4 to 1/3 of DW. Eye small, eyeball diameter 13.3–27.0% of preorbital snout length. Head long, its length about half of DW or more (48.5–59.5% of DW). Mouth without oral papillae. Dorsal surface of disc smooth in young, but with a row of five to nine prespine tubercles in adults. Dorsal and ventral tail folds present; ventral tail fold length about 3/4 of DW or more (71.5–90.7% of DW). Prespine separate centra 95–100, intestinal valve turns 16–18. Total pectoral radials 106–114, pelvic radials 17–19 in male and 20–23 in female. Both sexes mature at about 200–300 mm DW.

Dorsal surface of disc chocolate brown, and ventral surface whitish with brown margin. Ventral tail fold dark brown.

Distribution—Southern Japan to Indian Ocean. Found in relatively deep water.

Remarks—This species is most similar to *D. acutirostra* in its disc shape, but is clearly distinguishable from it by the following characters: eyeball diameter 13.3–27.0% of snout length in the present species (6.6–9.7% in *acutirostra*), presence of relatively distinct dorsal tail fold (usually absent), 106–114 total pectoral radials (129–135), 17–19 pelvic radials (23–25) in male and 20–23 (26–28) in female, 95–100 prespine separate centra (121–139), and 16–18 intestinal valve turns (22–24). Nishida andNakaya (1988a) designated the lectotype and paralectotypes for *D. zugei*. See Nishida and Nakaya (1988a) for detailed discussion of *D. zugei* and *D. acutirostra*.

Dasyatis brevis (Garman, 1880) (Fig. 11, Table 2)

Trygon brevis Garman, 1880: 171 (Payta, Peru).
Dasybatis dipterurus. Jordan and Gilbert, 1880: 31 (San Diego).
Dasyatis dipterura. Jordan and Evermann, 1896: 85.
Dasyatis hawaiensis. Jenkins, 1903: 420, pl. 1 (Honolulu, Hawaii).
Dasybatus brevis. Garman, 1913: 396, pl. 32, figs. 5, 6.
Dasyatis brevis. Fowler, 1929: 505.

Material Examined—LACM 31759-16, 225.1 mm DW, male, Baja California, Mexico.

Description—Disc rhomboid, anterior margin slightly convex and posterior margin convex. Outer corner of disc rounded. Snout blunt and not produced. Eye relatively large, with eyeball diameter about 2/3 of interorbital width. Dorsal surface of disc smooth in young. Adults with a row of midline tubercles and a short row of tubercles on each shoulder (Garman 1880). Tail less than 1.5 times disc length. Tail rough with asperities. A large specimen (457 mm DW) with three large erect, broad-based prespine tubercles (Garman 1880). Relatively high dorsal and ventral tail folds present. These folds occurring gradually and terminating abruptly. Prespine separate centra 124, pectoral radials 120, and pelvic radials 24 in a male specimen examined.

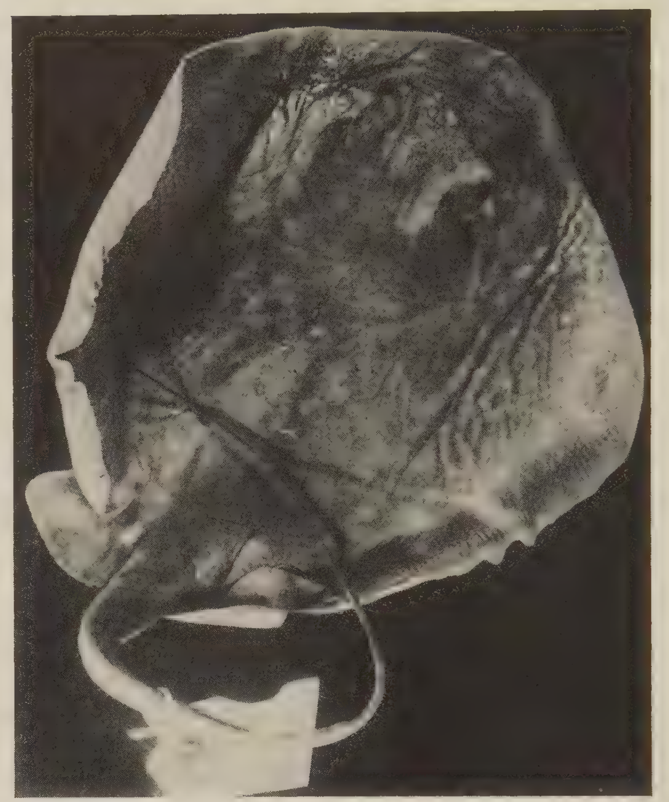

Figure 11.
Dasyatis brevis, 225.1 mm DW, male, LACM 31759-16.

Dorsal surface of disc olive brown, and ventral surface pale. Ventral tail fold black.

Distribution—Hawaii, California; Mexico; and Peru.

Remarks—Among the species with rhomboid discs and a dorsal tail fold or keel, *D. brevis* is most similar to *D. dipterura* (Jordan and Gilbert 1880) and *D. hawaiensis* Jenkins, 1903 in having relatively high tail folds and an entirely smooth disc when young. Garman (1913), and Beebe and Tee-Van (1941) synonymized *D. dipterura* with *D. brevis*. We compared the original description of *dipterura* with *brevis*, and could not find any specific differences between them. Thus, we also synonymize *D. dipterura* with *D. brevis*. Garman (1913) and Fowler (1941) examined the type specimen of *D. hawaiensis* and synonymized it with *D. brevis*. However, recently Gosline and Brock (1971) and Tinker (1978) used the name *D. hawaiensis*. According to the original description, *D. hawaiensis* has a short disc

(81.3% of DW) and wide interorbital region, which is 3.67 times the eye, 2 times the mouth, and 2 times the internasal length. However, our data for *D. brevis* show that it has a longer disc (88.9% of DW) and narrower interorbital region, which is 1.89 times the eye, 1.2 times the mouth, and 0.96 times the internasal length. These data indicate that the two species are distinct, but comparison of Jenkins's data with his original figure shows that his method of measurement apparently differs from ours. Although we could not examine the holotype, our measurements from the original figure of *D. hawaiensis* show that disc length is 87.6% of DW and interorbital region is about 1.7 times the eye. In fact, we could not find any significant differences between *D. brevis* and *D. hawaiensis*. Therefore, we follow Garman (1913) and Fowler (1941), who synonymized these species after their examination of the holotype of *D. hawaiensis*.

Dasyatis latus (Garman, 1880) (Fig. 12, Table 2)

Trygon lata Garman, 1880: 170 (Sandwich Islands).
Dasyatis sciera Jenkins, 1903: 421, pl. 1 (Honolulu, Hawaii).
Dasybatus latus. Garman, 1913: 383, pl. 32, figs. 1,2.
Dasyatis latus. Fowler, 1929: 505.

Material Examined—None.
The following description is cited from Garman (1880).

Description—Disc quadrangular, 1/4 wider than long. Anterior margins nearly straight, forming a very blunt angle at the snout, rounded near the outer extremities; posterior convex; inner straight a portion of their length. Ventrals truncate, rounded. Snout produced, forming a rounded prominence in front of the margins of the disc; length from forehead less than the width of the head. A line joining the wider portions of the disc passes nearer to the head than to the shoulders. Tail more than twice as long as the body, subcylindrical, without a trace of keel above, roughened with small tubercles, with an irregular series of broad-based conical tubercles on each side; a long narrow cutaneous expansion below has its origin opposite that of the spine, and terminates in a keel which continues to the extremity. A pair of large compressed erect tubercles stand immediately in front of the caudal spine, and a single one is placed over the middle of the pelvic arch; these suggest a continuous series in larger specimens. Three larger elongated tubercles with points directed backward—similar to those of *hastata*—occupy the middle of the shoulder girdle. Mouth curved, six (5–6?) papillae at the bottom; two of these are inthe middle in front where usually there is but one.

Color light olive, probably greenish in life, white below. Distinguished from *D. centrura* by the prominent snout, the shape of the tubercles on the middle of the back, and the narrowness of the posterior portion of the disc.

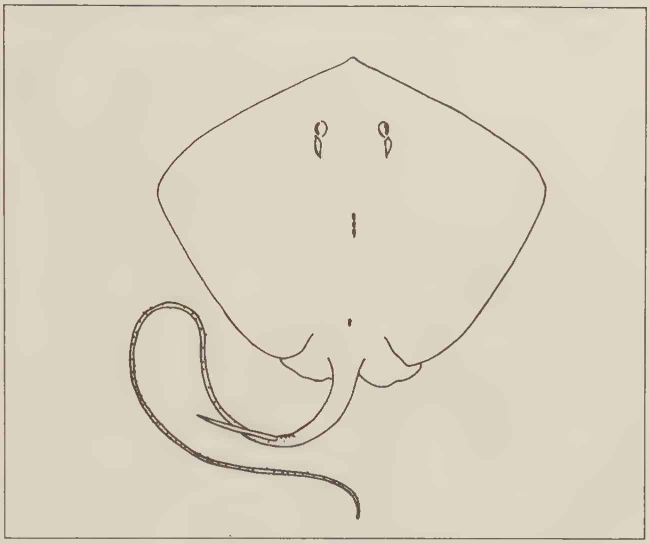

Figure 12.
Dasyatis latus, holotype, 520.7 mm DW, female, redrawn from Garman (1913).

Length of body 16 [406 mm], length of tail 35.3 [897 mm], and width of pectorals 20.5 [521 mm] inches. Collected at the Sandwich Islands by Andrew Garrett.

Distribution—Hawaii and Taiwan.

Remarks—Jenkins (1903) described *D. sciera* from Honolulu, Hawaii, but Garman (1913) and later Fowler (1941) synonymized *D. sciera* with *D. latus*, based on the examination of the type specimen of *D. sciera*. We follow their conclusion.

Dasyatis longus (Garman, 1880) (Fig. 13, Table 2)

Trygon longa Garman, 1880: 170 (Acapulco, Mexico; Panama).
Dasyabatus longus. Garman, 1913: 390, pl. 32, figs. 3, 4.
Dasyatis longus. Fowler, 1929: 505.

Material Examined—None.
The following description is cited from Garman (1880).

Description—Disc quadrangular, about 1/6 wider than long. Margins nearly straight, anterior meeting in a blunt angle on the end of the snout. Outer angles rounded, posterior blunt. Ventrals rounded. Tail more than twice as long as the body, roughened with small asperities, depressed anteriorly, compressed behind the spine, keeled above the compressed portion, with a long narrow cutaneous expansion on the lower side. Mouth curved, with five papillae. A row of small tubercles behind the head on the shoulder girdle. It is likely that large specimens are provided with tubercles on back and tail.

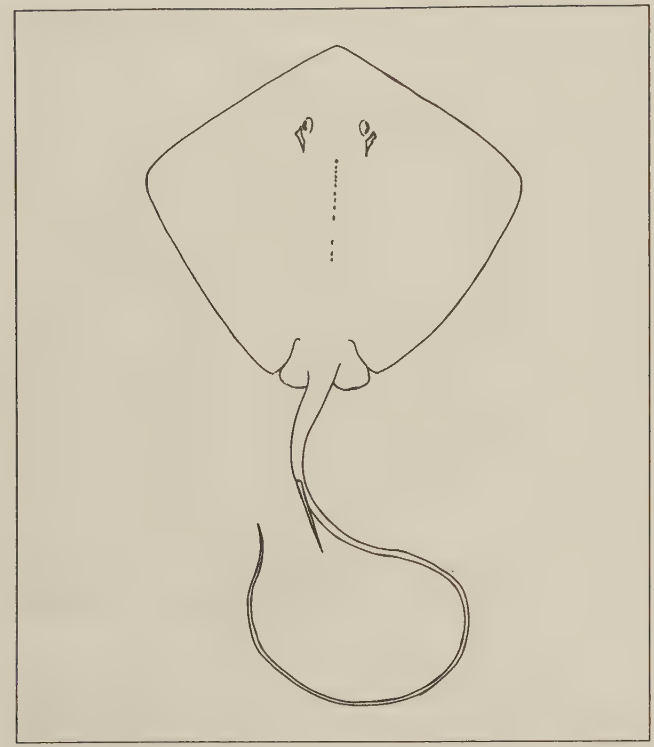

Figure 13.
Dasyatis longus, syntype, 350.5 mm DW, female, redrawn from Garman (1913).

Distinguished from *D. lata* by the shape of the disc and snout, and the keel on the tail; from *D. centrura* by the straight margins of the pectorals and the keel.

One specimen secured at Acapulco, Mexico, by Prof. Alexander Agassiz. One light-colored, reddish-brown specimen from Panama, by the Hassler Expedition.

Length of body 11.5 [292 mm], length of tail 28 [711 mm], and width of pectorals 13.8 [351 mm] inches. Length of body of second specimen 9.3 [236 mm], length of tail 24.5 [622 mm], and width of pectorals 11.2 [284 mm] inches.

Distribution—Gulf of California to the Galapagos.

Dasyatis navarrae (Steindachner, 1892) (Fig. 14, Table 2)

Trygon navarrae Steindachner, 1892a: 132 (Shanghai).
Dasyatis bennetti (not of Müller and Henle). Jordan and Richardson, 1909: 164, pl. 65.
Dasybatus navarrae. Garman, 1913: 393.
Dasyatis navarrae. Fowler, 1929: 505.

Material Examined—NMW 76571, holotype, 316 mm DW, male, Shanghai. The holotype was measured for us by Dr. Herzig (NMW).

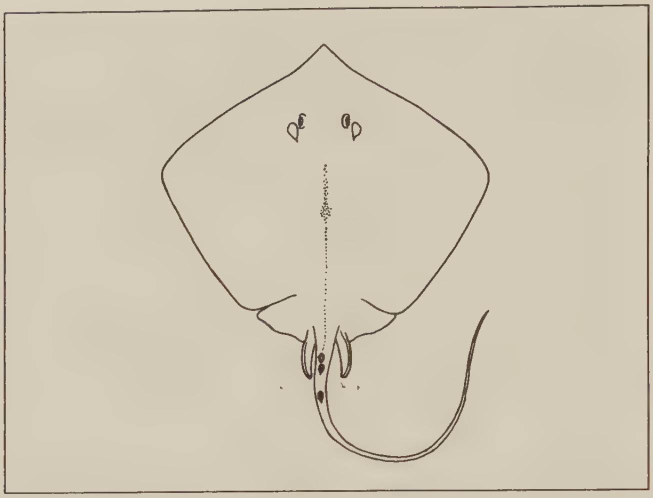

Figure 14.
Dasyatis navarrae, holotype, 316 mm DW, male, redrawn from Steindachner (1892b).

Description—Disc rhomboid, anterior margin of disc nearly straight and posterior margin slightly convex. Snout triangular and produced. Disc relatively long, its length 94.9% of DW, precloacal length 92.1% of DW. Snout about 1/4 (25.4%) of DW, and head length about half (52.8%) of DW. Eye small, eyeball diameter about 1/3 of interorbital width. Oral papillae 0-3-0; upper jaw teeth 40, lower jaw teeth 37. Middorsal part of disc covered with a band of small denticles. Tail with three large prespine tubercles. Prespine length very long and greater than DW (128.8% of DW). Dorsal and ventral tail folds present. Ventral tail fold relatively long, its length half (50%) of DW.

Dorsal surface of disc uniformly chocolate brown and ventral surface pale. Ventral tail fold blackish.

Distibution—Taiwan and Shanghai, China.

Dasyatis sinensis (Steindachner, 1892) (Fig. 15, Table 2)

Trygon sinensis Steindachner, 1892a: 133 (Shanghai).
Dasybatus sinensis. Garman, 1913: 393.
Dasyatis sinensis. Fowler, 1929: 505.

Material Examined—NMW 78600, holotype, 380 mm DW, male, Shanghai. The holotype was measured for us by Dr. Herzig (NMW).

Description—Disc rhomboid, anterior and posterior margins of disc slightly convex. Snout triangular and produced. Disc length 95.5% of DW, precloacal length 82.4% of DW. Snout length about 1/4 (24.9%) of DW, head length shorter than half (45.5%) of DW. Eyeball diameter about

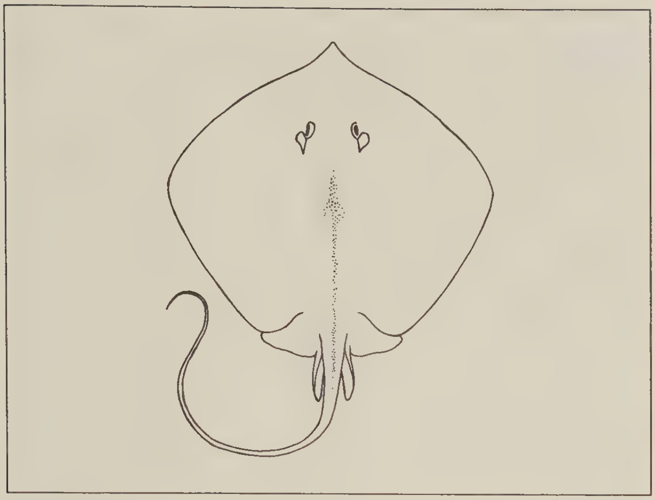

Figure 15.
Dasyatis sinensis, holotype, 380 mm DW, male, redrawn from Steindachner (1892b).

half of interorbital width. Oral papillae 1-3-1; upper jaw teeth 37, lower jaw teeth 40. Total pectoral radials 106, and pelvic radials 23 in male. Dorsal surface of disc and prespine region of tail covered with a band of small mid-dorsal denticles. Dorsal and ventral tail folds present. Ventral tail fold length shorter than half (45.0%) of DW.

Dorsal surface of disc gray with yellowish margin.

Dasyatis ushiei Jordan and Hubbs, 1925 (Fig. 16, Table 2)

Dasyatis ushiei Jordan and Hubbs, 1925: 114 (Mikawa Bay, Aichi Pref., Japan).

Material Examined—FMNH 59380 (Carnegie Museum 7778), holotype, 367 mm DW, male, Mikawa Bay, Aichi Pref., Japan.

Description—Disc rhomboid, anterior margin slightly convex and posterior margin convex. Disc about 4/5 (81.6%) of DW, precloacal length about 2/3 (71.1%) of DW. Snout blunt, its front angle 150 degrees. Snout about 1/6 (16.9%) of DW, head length 41.7% of DW. Eye of moderate size, eyeball diameter about half of interorbital width. Oral papillae 2-3-2; upper jaw teeth 42, lower jaw teeth 45. Disc entirely smooth at 367 mm DW. Prespine length short (107.6% of DW). Tail longer than twice disc length. Dorsal tail keel and ventral tail fold present. Ventral tail fold relatively long (42.2% of DW).

Dorsal surface of disc pale brown (gray with an irregular blackish margin according to the original description) and ventral surface whitish with darker margin.

Distribution—Reported from Mikawa Bay, Aichi Pref., Japan.

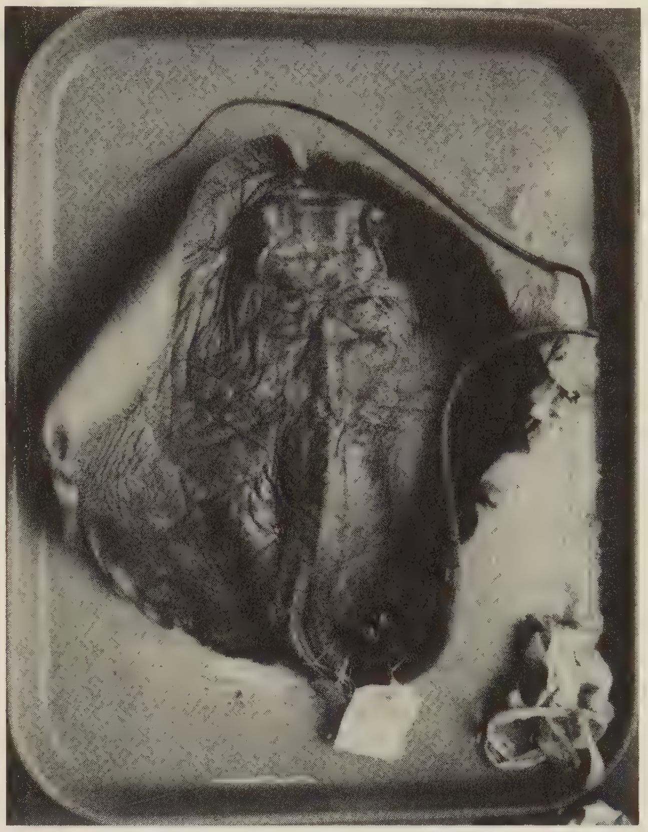

Figure 16.
Dasyatis ushiei, holotype, 367 mm DW, male, FMNH 59380 (Carnegie Museum 7778).

Remarks—According to Jordan and Hubbs (1925), *D. ushiei* is characterized by its large size, smooth body, shape and keeling of the tail, numerous (seven) oral papillae, blunt snout, etc. However, because of their relatively poor original description and small size of the holotype, *D. ushiei* is still very poorly known even in its type locality, Japan. Jordan and Hubbs (1925) identified a stuffed large specimen in the Ise Jingu Historical and Agricultural Museum (formerly, Yamada Museum) as *D. ushiei*, but this specimen resembles *D. matsubarai* in a number of characters including the presence of white spots on the dorsal surface of the disc. The holotype of *D. ushiei* lacks white spots on its body.

The holotype of *D. ushiei* (367 mm DW) has small and soft claspers in spite of its relatively large size, suggesting that *D. ushiei* is a large stingray. However, we have never obtained any specimen which can confidently be identified as *D. ushiei*. Nakaya (1984) used a photograph of a large stingray (1329 mm DW) taken from Izu Oshima, Japan under the name of *D. ushiei*, but it cannot positively be identified as *D. ushiei* because of the large size difference between this specimen and the holotype.

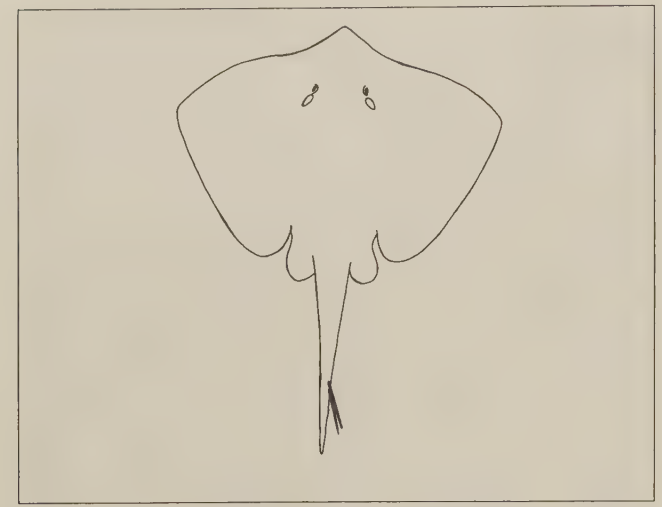

Figure 17.
Dasyatis giganteus, holotype, 1780 mm DW, female, redrawn from Soldatov and Lindberg (1930).

Dasyatis giganteus (Lindberg, 1930) (Fig. 17, Table 2)

Urolophoides giganteus Lindberg in Soldatov and Lindberg, 1930: 26, fig. 4 (Basargin Cape, Peter the Great Bay).

Material Examined—None.

The following is cited from the original description (Lindberg in Soldatov and Lindberg 1930) based on a stuffed specimen (1780 mm DW).

Description—Disc much broader than long, longer than tail. Greatest breadth of disc about opposite 2/5 of length of disc, measured from tip of snout to posterior border of pectoral. Snout (measured from eyes) longer than the width of the interorbital space, equal to 1/4 of disc. Diameter of eye shorter than the spiracles, 12 in snout [*sic*]. Width of mouth about 2 in snout [*sic*] before it. Ventrals projecting beyond disc. Tail short, stout and blunt on the tip: its length 72.9% to length of disc; upper part of tail covered with numerous small prickles; two strong spines at base of tail and two ones [*sic*] at the beginning 2/3; two large caudal needles in middle of tail. Caudle needles slightly longer than the width of the interorbital space; very strong and serrated, inserted behind middle of tail. Dorsal and caudal fins none. The vertical membranous fold on the upper surface of the tail. Skin of disc smooth, except posterior parts of pectoral and ventral fins.

Distribution—Recorded from Basargin Cape, Peter the Great Bay and off Askold Island.

Remarks—In the original description of *U. giganteus*, Lindberg stated that there was a vertical membranous fold on the upper surface of the tail. Later Lindberg and Legeza (1959, fig. 90) illustrated the holotype and stated that *U. giganteus* has no dorsal tail fold. Because we could not examine the type specimen, we are unable to verify the existence of a dorsal tail told. We tentatively follow the original description (dorsal tail fold present).

Among species with a rhomboid disc and a dorsal tail fold, this species is characterized by having relatively long snout length (20.2% of DW), very short head length (27.5% of DW), and relatively wide interorbital width (13.5% of DW).

Dasyatis matsubarai Miyosi, 1939 (Figs. 18, 19; Table 2)

Dasyatis matsubarai Miyosi, 1939: 46, text-fig. 3 (Hyuga Nada, Miyazaki Pref., Japan).

Urolophoides matsubarai. Lindberg and Legeza, 1959: 134, fig. 88.

Urolophoides multispinosus Tokarev in Lindberg and Legeza, 1959: 135, fig. 89 (140 miles south of Cape Gamov, Sea of Japan).

Material Examined—HUMZ 35030, 435.2 mm DW, male, Funka Bay, Hokkaido Pref., Japan; HUMZ 60208, 436.7 mm DW, male, Minamikayabe, Hokkaido Pref., Japan; HUMZ 65256, 417.6 mm DW, male, Minamikayabe, Hokkaido Pref., Japan; HUMZ 82490, 393.4 mm DW, male, Minamikayabe, Hokkaido Pref., Japan; HUMZ 90772, 347.8 mm DW, male, Minamikayabe, Hokkaido Pref., Japan; HUMZ 98825, 429.9 mm DW, male Minamikayabe, Hokkaido Pref., Japan; HUMZ 105477, 105478, 389.0, 394.6 mm DW, 2 males, off Numazu, Shizuoka Pref., Japan; HUMZ 111744-111746, 337.8-427.1 mm DW, 3 males, off Numazu, Shizuoka Pref., Japan; USNM 71903, 324.8 mm DW, male Misaki, Kanagawa Pref., Japan; HUMZ 35022, 407.0 mm DW, female, Japan; HUMZ 35032, 444.1 mm DW, female, Funka Bay, Hokkaido Pref., Japan; HUMZ 70808, 477.5 mm DW, female, Minamikayabe, Hokkaido Pref., Japan; HUMZ 75751, 361.7 mm DW, female, Minamikayabe, Hokkaido Pref., Japan; HUMZ 105479, 387.5 mm DW, female, off Numazu, Shizuoka Pref., Japan; HUMZ 105481, 105482, 397.8, 367.9 mm DW, 2 females, off Numazu, Shizuoka Pref., Japan; HUMZ 106269, 395.2 mm DW, female, off Numazu, Shizuoka Pref., Japan; HUMZ 111747, 405.0 mm DW, female, off Numazu, Shizuoka Pref., Japan, MSM-80-47, 1018.0 mm DW, female, Kozu Island, Tokyo Pref., Japan; Uncatalogued specimen of the Ise Jingu Historical and Agricultural Museum, 958.0 mm DW, female, Iwasaki, Mutsu Bay, Aomori Pref., Japan; HUMZ 111748, 1830 mm DW, female, off Cape Erimo, Hokkaido Pref., Japan.

Description—Disc rhomboid, anterior margin nearly

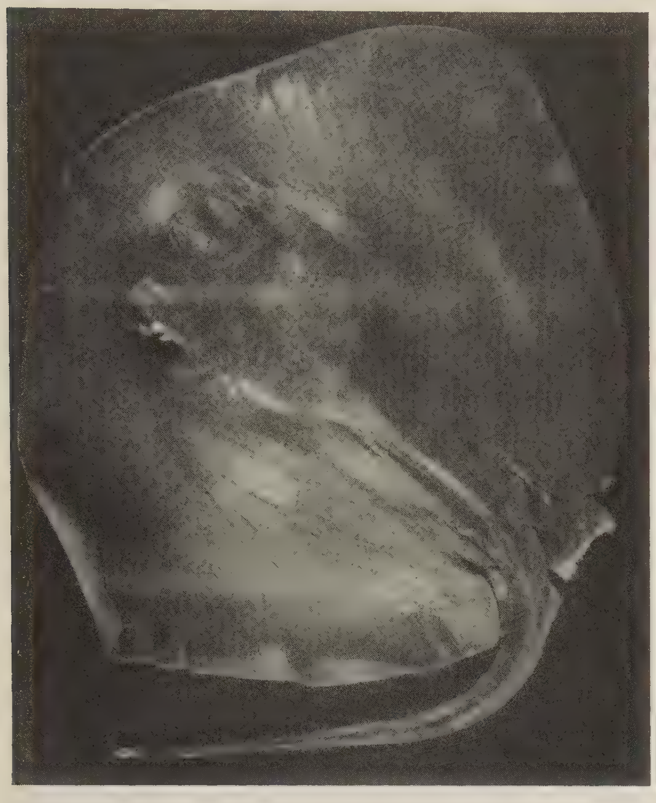

Figure 18.
Dasyatis matsubarai, 395.2 mm DW, female, HUMZ 106269.

straight and posterior margin convex. Snout angular and not produced. Precloacal length relatively short (68.2–75.2% of DW). Oral papillae 0-0-0 to 3-7-2 (Table 1); upper jaw teeth 34–44, lower jaw teeth 33–46. Intestinal valve turns 25–26, prespine separate centra 113–129, total pectoral radials 120–124, pelvic radials 18–20 in male and 26 in female. Dorsal surface of the disc smooth in young, but in adults disc with a row of three to five midline tubercles and tip of snout with two to ten tubercles. An anteriorly curved groove present on ventral side of disc just behind pectoral girdle (Fig. 19). Tail variable in length (tail length 75.3–122.0% of DW), with one to eight prespine tubercles in adults, and tail rough with asperities distally. Dorsal tail keel and ventral tail fold present. Ventral tail fold length 31.0–44.0% of DW.

Dorsal surface of disc dark gray with many pores surrounded with white color. Ventral surface of disc white with gray margin and gray irregular spots. Ventral tail fold blackish.

Distribution—Japanese waters, especially common in Hokkaido and northern Honshu.

Remarks—Tokarev described *D. multispinosus* from the Japan Ses. However this species cannot be distinguished from *D. matsubarai*. Like *D. matsubarai* it possesses white spots on the disc, short total length (154.1% of DW), and disc width about 110% of disc length. In addition, the figure of *D. multispinosus* (Lindberg and Legeza 1959, fig. 89) shows that it has an anteriorlly curved groove on ventral side of the disc at the pectoral girdle, which is a typical character of *D. matsubarai* (see below). *D. multispinosus* is also characterized by having three tail spines, but *D. matsubarai* has one to three tail spines. As shown above, we could not find any differences between *multispinosus* and *matsubarai*, and we regard *D. multispinosus* as a junior synonym of *D. matsubarai*.

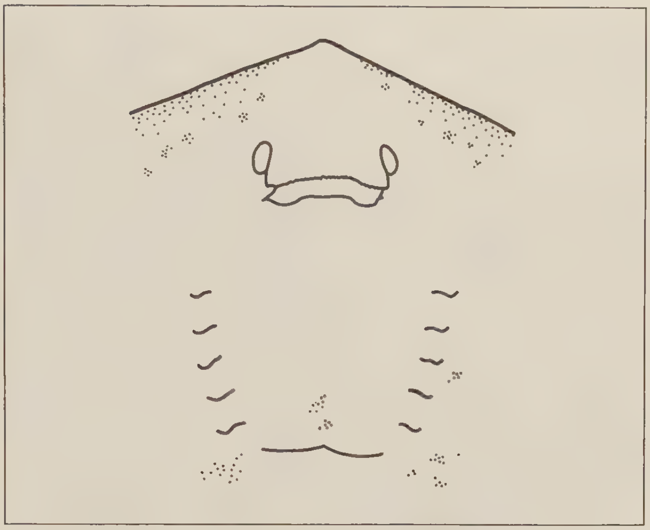

Figure 19.
Anteriorly curved groove on ventral side of disc in *Dasyatis matsubarai*.

All the examined specimens of *D. matsubarai* have an anteriorly curved groove on the ventral side of the disc just behind the pectoral girdle (Fig. 19) and this groove is unknown in any other species of the genus. Therefore, the groove is a very useful taxonomic character in *D. matsubarai*.

This species is most similar to *D. akajei* and *D. ushiei* in its general appearance. In fact, some specimens of *D. matsubarai* are misidentified as *D. akajei* (e.g., USNM 71903 by Fowler 1941) or *D. ushiei* (in some aquaria in Japan). However, it is easily distinguishable from them by its dark gray color, white spots on the dorsal surface and an anteriorly curved groove on the ventral side of the disc.

Dasyatis laevigatus Chu, 1960 (Table 2)

Dasyatis laevigatus Chu, 1960: 170, figs. 160–162 (Shanghai Fish Market, Dongfushan, Huaniao).

Material Examined—None.

The following is a translation of the original description (Chu 1960) written in Chinese.

Description—Disc subrhomboid, anterior margin straight and slightly concave near the outer side of eyes; snouth angle about 60°, outer and posterior corners rounded. Disc width 1.2–1.3 times disc length. A line formed by the greatest disc width lies anterior to a parallel line drawn through the midpoint of the disc length. Snout moderately long and angular, its length about 2/9 of disc length. Eye large and protruding, eyeball diameter equal to or slightly greater than spiracle, about 2/3 of interorbital width. Interorbital region flat, its width about half of snout. Nostrils forming a single rectangular curtain with a straight and fringed posterior margin reaching to the lower jaw, (posterior nasal flat not developed) spiracles elliptical. The mouth small, transverse and undulate, the symphysis of the upper jaw protruding and both sides indented. The lower jaw indented at symphysis and protruding on both sides. Preoral snout length 2.4–2.7 times mouth width; palate membrane developed, its posterior margin fringed and roundly indented; oral papillae three (0,1,1,1,0). Teeth small and flat, arranged in quincunx; female teeth flat and blunt without a cusp, male teeth with a sharp cusp directed backward, upper jaw teeth about 40. Spiracle elliptical, located just behind eye, its anterior margin extending to the lower rear corner of the eye, and with a membrane inside which can open and close the spiracle. Gill openings five, narrow and small, each interbranchial width about the same, and each gill opening length about the same, 5th interbranchial width about 3.5 times the 3rd gill opening length.

Pelvic fin nearly rectangular or square; in males, anterior and posterior margins straight, inner margin short and clear; clasper depressed and its tip blunt; in females, pelvic fins wider, anterior margin straight, posterior and inner margins combined and forming a widely rounded margin. Tail relatively short, its length about 1.4–1.8 times disc length, anterior half compressed, posterior half whip-like; dorsal and ventral tail folds present; dorsal tail fold short, occurring posteriorly to tail spine, its length about same as tail spine length; ventral tail fold wider and longer, its length about 2/5 of tail length.

Body entirely smooth even in large males and females. Dorsal surface of disc yellowish gray brown with irregular dark spots; anterior and ventral parts of eye, and dorsal part of spiracle white (yellow in a fresh specimen). Ventral surface of pectoral and pelvic fins white with yellowish gray margin and irregular gray brown spots. Anterior part of tail gray brown; posterior part dark brown with pale yellow lateral margin; dorsal and ventral tail folds black.

Distribution—China and Taiwan.

Remarks—This species is characterized by its entirely smooth body even in the adult, short disc (76.9–83.3% of DW), yellowish gray brown dorsal surface of disc with irregular dark spots, and ventral surface of disc with yellowish gray margin and irregular gray brown spots.

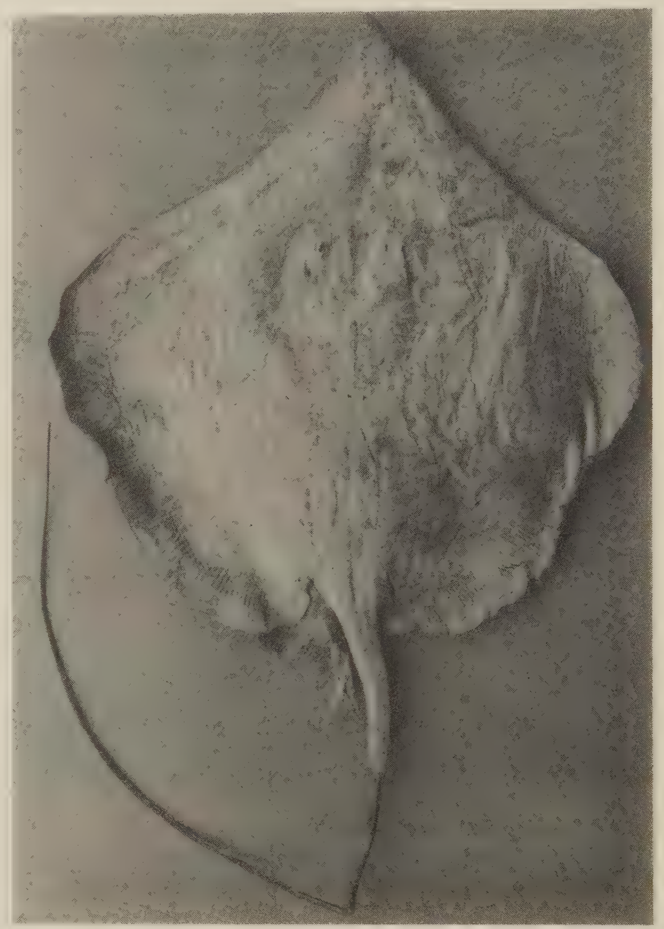

Figure 20.
Dasyatis acutirostra, holotype, 724.8 mm DW, male, HUMZ 97435.

Dasyatis acutirostra Nishida and Nakaya, 1988 (Fig. 20, Table 2)

Dasyatis zugei (not of Müller and Henle). Jordan and Fowler, 1903: 660 (in part).

Dasybatus zugei (not of Müller and Henle). Garman, 1913: 398 (in part).

Dasyatis microphthalmus (not of Chen). Chu, 1960: 165, figs. 153–155.

Dasyatis bennettii (not of Müller and Henle). Faculty of Fisheries, University of Nagasaki, 1973: 399, pl. 20.

Dasyatis acutirostra. Nishida and Nakaya, 1988a: 115, figs. 1, 2.

Material Examined—HUMZ 97435, holotype, 724.8 mm DW, male, 30°09′–31°30′N, 124°13′–127°53′E, East China Sea; HUMZ 107583–107599, paratypes, 281.4–348.2 mm DW, 8 males and 9 females, Japan; FAKU 101210, paratype, 354.2 mm DW, male, Japan; USNM 51358, paratype, 287 mm DW, male, Kobe, Hyogo Pref., Japan; MTUF 25267, paratype, 515.6 mm DW, female, Nagasaki, Nagasaki Pref., Japan.

Description—Disc rhomboid with extremely elongate snout, anterior margin concave and posterior margin convex. Disc length about same as DW (99.1–106.1% of DW). Head longer than half (56.0–63.0%) of DW. Snout longer than 1/3 (36.9–43.9%) of DW. Eye small, eyeball diameter 10–16.3 in snout length and 2.5–4.0 in interorbital width. Floor of mouth without oral papillae. Dorsal surface of disc and tail smooth in young specimens, but with a row of 30 midline and 16 prespine tubercles in adults. Dorsal tail keel usually absent (if present very inconspicuous), but ventral tail fold present. Ventral tail fold short, its length 15.0–22.9% of DW. Tail distally rough with small aspertities. Prespine separate centra 121–139, pectoral radials 129–135, pelvic radials 23–25 in male and 26–28 in female, intestinal valve turns 22–24.

Dorsal surface of disc pale brown, and ventral surface whitish after preservation in formalin. Ventral tail fold pale brown.

Distribution—East China Sea and off the coast of southern Japan.

Remarks—*D. acutirostra* is most similar to *D. zugei* in disc shape, but has much longer snout and smaller eyes. See remarks in the account of *D. zugei* above and in Nishida and Nakaya (1988a) for further comparisons.

Dasyatis izuensis Nishida and Nakaya, 1988 (Fig. 21, Table 2)

Dasyatis izuensis Nishida and Nakaya, 1988b; 227, figs. 1–4.

Material Examined—HUMZ 109730, hologype, 418.2 mm DW, male, Shimoda Bay, Shizuoka Pref., Japan; HUMZ 109731, paratype, 375.0 mm DW, male, off Shirahama, Shizuoka Pref., Japan; HUMZ 109732, 109733, paratypes, 182.9, 197.2 mm DW, 2 males, Shimoda Bay, Shizuoka Pref., Japan; HUMZ 109716, paratype, 362.0 mm DW, male, off Numazu, Shizuoka Pref., Japan; HUMZ 105476, paratype, 367.5 mm DW, female, off Numazu, Shizuoka Pref., Japn; HUMZ 105907, paratype, 228.3 mm DW, female, off Itado, Shizuoka Pref., Japan; HUMZ 107444, paratype, 182.6 mm DW, female, Shimoda Bay, Shizuoka Pref., Japan.

Description—Disc rhomboid and moderately thick, anterior and posterior margins of disc slightly convex. Snout short, its length 14.1–18.7% of DW. Interorbital width half (or more) of snout length. Eye relatively large, eyeball diameter about half (or more) of interorbital width. Dorsal surface of disc smooth even in adults. Only one row of two to six small prespine tubercles present in adults. Dorsal tail keel and ventral tail fold present. Ventral tail fold short, its length shorter than 1/3 of DW. Tail short, its length about same as disc length. Prespine separate centra 101–110, intestinal valve turns 18–20, pelvic radials 20–21 in males and 26–27 in females.

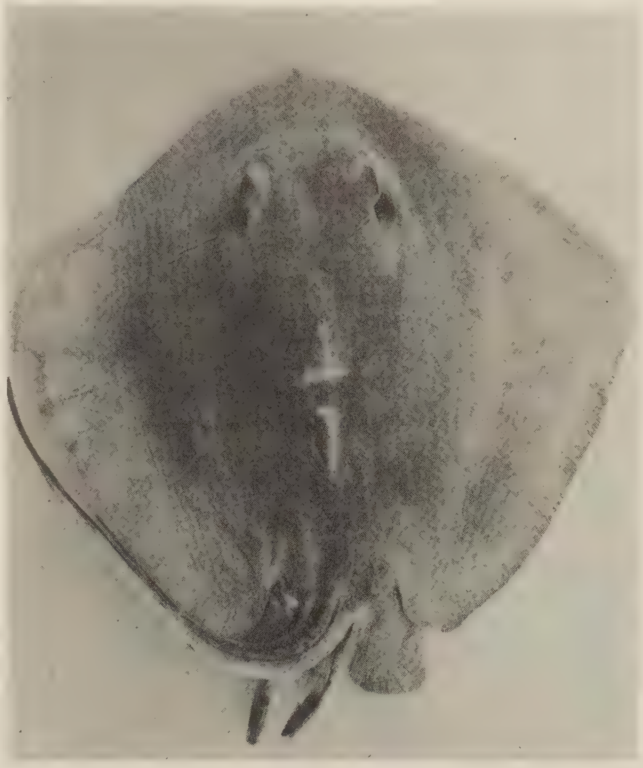

Figure 21.
Dasyatis izuensis, holotype, 418.2 mm DW, male, HUMZ 109730.

Dorsal surface of disc golden brown in fresh specimens, and ventral surface white with gray posterior margin. Ventral tail fold white.

Distribution—Izu Peninsula, Pacific coast of Japan. Collected by gill net only from shallow coastal waters.

Remarks—*D. izuensis* is clearly distinguishable from other species with a rhomboid disc and dorsal tail fold or keel by having uniformly golden brown dorsal disc, and a short (shorter than 1/3 of DW) white ventral tail fold. See Nishida and Nakaya (1988b) for detailed information on this species.

Dasyatis sp. 1 (Fig. 22, Table 2)

Material Examined—HUMZ 107700, 530.1 mm DW, female. Daxi Fish Market, Taiwan.

Description—Disc rhomboid and wide, its width about 120% of length. Snout rounded and not produced. Anterior margin of disc slightly concave and posterior margin convex. Snout short, its length shorter than 1/5 (16.7%) of DW; head length 38.3% of DW. Dorsal surface of disc

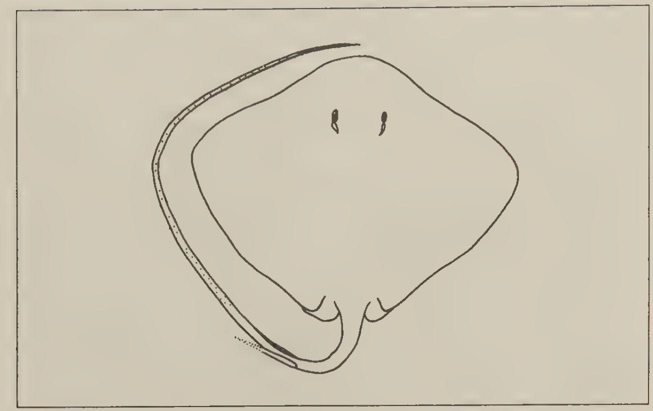

Figure 22.
Dasyatis sp. 1, 530.1 mm DW, female, HUMZ 107700.

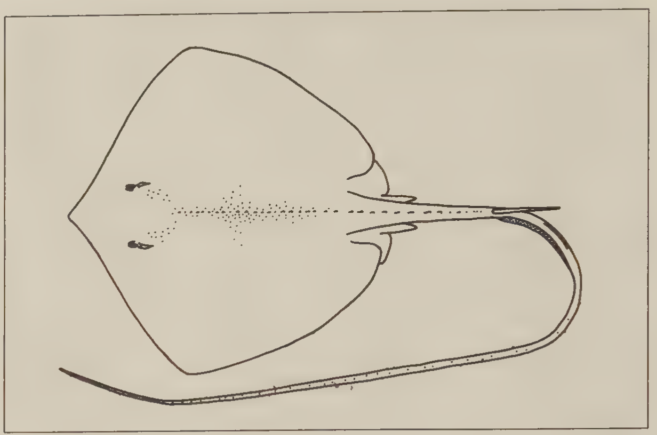

Figure 23.
Dasyatis sp. 2, 437.2 mm DW, male HUMZ 109484.

smooth. Tail without prespine tubercles, but distally rough with asperities. Prespine length short, about same as DW (101.4% of DW). Dorsal tail fold or keel absent, but ventral tail fold present. Oral papillae 2-3-2; upper jaw teeth 39, lower jaw teeth 45. Pectoral radials 129, intestinal valve turns 26, pelvic radials 28 in a female.

Dorsal surface of disc uniformly greenish brown, and ventral surface white with dark gray margin. Ventral tail fold dark gray.

Remarks—This specimen was collected at Daxi Fish Market, Taiwan by the first author. It is most similar to *D. latus* in disc shape and absence of dorsal tail fold or keel, but distinguishable from the latter species by having an undulate anterior margin of the disc and a shorter prespine length.

Dasyatis sp. 2 (Fig. 23, Table 2)

Material Examined—HUMZ 109484, 437.2 mm DW, male, Zhongzhou Fish Market, Taiwan.

Description—Disc rhomboid, anterior and posterior margins of disc slightly convex. Snout triangular and slightly produced. Dorsal surface of disc with a row of midline tubercles, postorbital, middorsal, and shoulder regions covered by small denticles, and a row of prespine tubercles also present. Oral papillae 1-3-1; upper jaw teeth 51, lower jaw teeth 49. Pectoral radials 109, pelvic radials 19 in a male. Tail longer than twice the disc length and distally rough with asperities. Prespine length 127.3% of DW. Dorsal tail keel and ventral tail fold present. Ventral tail fold longer than half (64.1%) of DW.

Dorsal surface of disc uniformly chocolate brown, and ventral surface whitish. The ventral tail fold is blackish.

Remarks—This specimen was collected at Zhongzhou Fish Market, Taiwan by the first author. It differs from other species with a rhomboid disc and dorsal tail keel by having a combination of the following characters: tail longer than twice the disc length, long prespine length, ventral tail fold longer than half of DW, and uniformly chocolate brown coloration on dorsal surface of the disc.

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Interrelationships of the Etmopterinae (Chondrichthyes, Squaliformes)

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ABSTRACT

A cladistic analysis of the etmopterine sharks was conducted based on skeletal, muscular, and external characters using the outgroup rule. Within the Squaliformes, the subfamily Etmopterinae should be recognized as a monophyletic group by having the following autapomorphies: keel-process of basal cranii present, and labial cartilages composed of two separate parts. The present study indicates that *Etmopterus* + *Centroscyllium sheikoi*, and the rest of *Centroscyllium* + *Aculeola* are sister groups. These findings necessitate that *C. sheikoi* must be raised to the generic rank (*Miroscyllium*). Diagnostic characters are given for these natural taxa.

Introduction

The Squaliformes, equivalent to the Squaloidea of Bigelow and Schroeder (1957), traditionally has been divided into subgroups based on the presence or absence of dorsal fin spines. This subdivision led to the definition of two higher taxa, the Squalidae and Dalatiidae (sometimes regarded as subfamilies of the Squalidae); the Echinorhinidae was sometimes recognized separately as well. Hubbs and McHugh (1951) inferred that the loss of fin spines had occurred in more than one phyletic line and suggested that these subgroups were artificial and unnatural. Bigelow and Schroeder (1957), however, retained the traditional classification, because there seemed to be no securely objective basis for the subdivision of this group, and because they emphasized convenience in classification over phylogenetic implications. Their review is still the most comprehensive account of this group, and most subsequent workers have continued to use their scheme of squaliform classification.

Recently, Compagno (1973, 1977) introduced an "eclectic and provisional" taxonomic system based on the phylogenetic scheme and all-around comparisons of character conditions among living elasmobranchs. He recognized two higher taxa, Echinorhinidae, for the genus *Echinorhinus*, and Squalidae for the rest of the order, and he erected six subfamilies in the latter (later amended to four or five in Compagno 1984).

We have collected much information in an effort to elucidate squaliform phylogeny and suggest that a small group equivalent to the Etmopterinae of Compagno (1973, 1984) and Cadenat and Blache (1981) should be recognized. This higher taxon is composed of three known genera, *Etmopterus*, *Centroscyllium*, and *Aculeola*, and is not equal to the Etmopterinae of Fowler (1934), which included a large part of the squalids sharing grooved fin spines and a distinct subterminal notch of the caudal fin. We made this study in order to a) investigate monophyly of Etmopterinae, b) analyze the interrelationships of this group, and c) elucidate taxonomic changes and give diagnostic characters for each taxa.

Materials and Methods

Two major principles were applied to examine phylogenetic relationships: Hennig's principle of synapomorphy (1966) and Nelson's principle of parsimony (1970). The polarity of each morphocline of characters was determined by the outgroup rule (Wiley 1981). The phylogenetic relationships which are the basis of the present character analysis were taken from the superorder Squalomorphii of Compagno (1973, 1977). Some authors have questioned his synapomorphies (e.g., Maisey 1980); however, we consider only Compagno's scheme to be useful in the context of this study because no other study has paid attention to squaliform monophyly. We investigated the character distributions of the squalomorph species as much as possible in order to ascertain polarity. Since Compagno (1973, 1977) did not refer to the relationships of the six squalid subfamilies, we estimated the conditions of the common ancestor of the

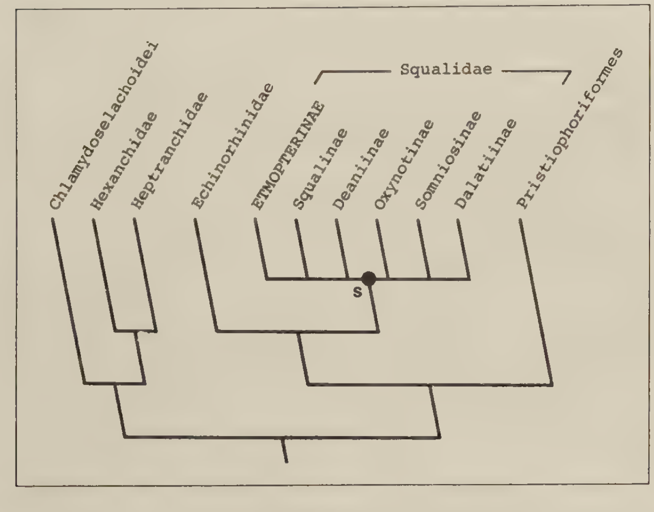

Figure 1.
The phylogenetic relationships used in the present character analysis (based on Compagno 1973, 1977). Node S shows the common ancestor of his Squalidae, which was estimated to examine both monophyly of Etmopterinae and its interrelationships.

Etmopterinae from those of the Squalidae to examine both monophyly of Etmopterinae and its interrelationships (Fig. 1).

External structures, skeletal, and muscular systems of whole sharks were examined. Illustrations were drawn using a camera lucida from cleared and stained specimens prepared by the method of Dingerkus and Uhler (1977). Terminology of skeletal and muscular systems mainly follow that of Edgeworth (1935) and Holmgren (1940, 1941). The terminology of Allis (1923), Daniel (1934), and Compagno (1973) are used as supplements. The study materials examined belong to the following collections of museums and institutions: FRSKU (Fisheries Research Station, Kyoto University, Maizuru); FSFL (Far Seas Fisheries Research Laboratory, Shimizu); HUMZ (Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University, Hakodate); NMNZ (National Museum of New Zealand, Wellington); NSMT (Department of Zoology, National Science Museum, Tokyo); RUSI (J.L.B. Smith Institute of Ichthyology, Grahamstown); SU (Natural History Museum, Stanford University [now housed in the California Academy of Sciences, San Francisco]); and USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C.).

Etmopterinae

Aculeola nigra—HUMZ 90412, 439 mm TL, male, off Chile; USNM 220266, 385 mm TL, male, off Peru.

Centroscyllium fabricii—FSFL 0863d, 500 mm TL, male, western North Atlantic; HUMZ 112559, 382 mm TL, male, west of Greenland (Davis Strait).

C. kamoharai—HUMZ 95207, 367 mm TL, male, East China Sea.

C. nigrum—HUMZ 110329, 380 mm TL, male, off California.

C. ritteri—HUMZ 72523, 485 mm TL, female, off Fukushima, Japan; HUMZ 93929, 412 mm TL, male, off Iwate, Japan (both western North Pacific).

C. sheikoi (= *Miroscyllium sheikoi*)—HUMZ 74977, 293 mm TL, male; HUMZ 74982, 399 mm TL, male; HUMZ 74984, 213 mm TL, male; all from Kyushu-Palau Ridge (western North Pacific).

Etmopterus baxteri—HUMZ 91313, 428 mm TL, female; HUMZ 91316, 457 mm TL, male; both south of New Zealand.

E. brachyurus—HUMZ 74601, 295 mm TL, male, western South Indian Ocean.

E. lucifer—HUMZ 34580, 355 mm TL, female, off Kochi, Japan (western North Pacific); HUMZ 74985, 355 mm TL, male, Kyushu-Palau Ridge; HUMZ 90230, 337 mm TL, male, off Fukushima, Japan.

E. pusillus—HUMZ 74595, 395 mm TL, male, western South Indian Ocean.

E. schultzi—NSMT-P 10944, 240 mm TL, male, off Patagonia.

E. spinax—FSFL-S 348, 292 mm TL, male, eastern Atlantic; SU 20617, 252 mm TL, male, off Italy Mediterranean.

E. unicolor—HUMZ 95257, 412 mm TL, female, East China Sea.

E. virens—SU 66821, 223 mm TL, male, the Gulf of Mexico.

Squalidae

Centrophorus acus—HUMZ 101726, 515 mm TL, male, off Okinawa Is., Japan.

C. granulosus—USNM 220221, 385 mm TL, male, Caribbean Sea.

C. uyato—HUMZ 90414, 659 mm TL, male, off western North Africa.

C. squamosus—HUMZ 87099, 453 mm TL, male, off western North Africa.

Centroscymnus crepidater—HUMZ 73509, 685 mm TL, male, off South Africa; FRSKU-S 1661, 554 mm TL, female, off Chile.

C. owstoni—NMNZ 2359, 582 mm TL, female, off New Zealand; HUMZ 101723, 652 mm TL, male, off Okinawa Is., Japan.

Cirrhigaleus barbifer—HUMZ 95177, 584 mm TL, female, East China Sea.

Dalatias licha—HUMZ 74603, 390 mm TL, male, off South Africa; HUMZ 95229, 621 mm TL, male, East China Sea.

Deania calcea—FRSKU-S 1662, 589 mm TL, female, off Chile.

Euprotomicrus bispinatus—HUMZ 90413, 197 mm TL, male, off Hawaii Is.

Isistius brasiliensis—HUMZ 86585, 480 mm TL, female; HUMZ 89900 516 mm TL, female; both from western North Pacific.

Oxynotus bruniensis—HUMZ 91383, 545 mm TL, male, off New Zealand.

O. centrina—FSFL-M 232, 350 mm TL, male, the Gulf of Guinea.

Somniosus pacificus—HUMZ 88828, 1,010 mm TL, male, south of Bering Sea.

Squaliolus laticaudus—HUMZ 74972, 250 mm TL, female; HUMZ 74974, 245 mm TL, female; both from Kyushu-Palau Ridge.

Squalus acanthias—HUMZ 87733, 495 mm TL, male, off Hokkaido, Japan (western North Pacific); HUMZ 91553, 525 mm TL, male, south of New Zealand.

S. asper—RUSI 6039, 225 mm TL, female, off South Africa.

S. blainvillei—HUMZ 95192, 825 mm TL, male, East China Sea.

S. japonicus—HUMZ 95213, 502 mm TL, male, East China Sea.

S. megalops—HUMZ 37664, 445 mm TL, female, off Borneo Is.

S. mitsukurii—HUMZ 68767, 620 mm TL, male, Emperor Seamount Chain.

Zameus squamulosus—HUMZ 75872, 526 mm TL, male, off New Zealand; HUMZ 95248, 435 mm TL, female, East China Sea.

Echinorhinidae

Echinorhinus cookei—USNM 179085, 178 mm TL, male, off California.

Pristiophoriformes

Pristiophorus japonicus—HUMZ 49349, 387 mm TL, male, off Kochi Pref., Japan.

P. nudipinnis—FSFL-EA 735, 687 mm TL, male, off south Australia.

Hexanchiformes

Chlamydoselachus anguineus—FSFL-D 2802, 652 mm TL, off South Africa.

Heptranchias perlo—HUMZ 101712, 542 mm TL, male, off Okinawa Is.

Hexanchus griseus—HUMZ 95104, 698 mm TL, male, East China Sea.

Notorynchus cepedianus—HUMZ 6749, 740 mm TL, female, Shimonoseki Fish Market, Japan.

Results and Discussion

Monophyly of Etmopterinae

The subfamily Etmopterinae, which includes three known genera: *Etmopterus*, *Centroscyllium*, and *Aculeola*, is characterized by two autapomorphies (the following numerical values noted in the parentheses identify each apomorphic character used in our reconstruction of etmopterine phylogeny, discussed later). The first is (1) anterior part of palatobasal process with a rod-like projection (keel-process of basis cranii: kp) extending anteroventrally related to articulation with palatoquadrate (Fig. 2). The keel part of ventral surface of ethmoid to orbital region is more or less developed in squalids (absent in echinorhinids, pristiophoriforms, and hexanchiforms), and in *Zameus*, *Squaliolus*, and *Euprotomicrus* this part expands subtriangularly and is probably involved in the ethmoid-orbital articulation. However, the condition of this part in etmopterines is unique among squaliforms because of its simple rod-like shape. The second autapomorphy is (2) labial cartilages (lc) composed of two separate parts, a prominent paddle-like lower cartilage and a short and slender upper one (Fig. 3). Other squalids and chlamydoselachoids have three developed labial cartilages, two of which are on the upper jaw and one on the lower, and the posterior upper and the lower cartilages are articulated in almost of all the species. In Pristiophoriformes and hexanchoids, one or two reduced pieces of cartilages are present on the upper jaw or may be absent in some cases.

This monophyletic group is equal to the Etmopterinae of Compagno (1973, 1984); however, he has not revealed the monophyly and character conditions of this group. Although we do not refer to the systematic position of the Etmopterinae within the family here (partly because the character distributions in the Squalidae are most complex), the two autapomorphic states noted above strongly support the monophyly of the Etmopterinae. Our phylogenetic study also shows two synapomorphies within the Etmopterinae which, although not autapomorphic, further strengthen the certainty of etmopterine monophyly [conditions of other squalomorphs in brackets]: (3) absence of a supraotic shelf (sos) for the origins of levator dorsalis and the most anterior part of the constrictor hyoideus dorsalis [other squalomorphs except for the genus *Isistius* have a developed supraotic shelf along the upper margin of otic region] (Fig. 2), and (4) second dorsal fin with more or less developed cartilaginous plates or pieces anterior to the fin spine (prespinal radials) [also observed only in the genus *Squalus*].

As Burgess and Springer (1986) pointed out, it appears that the distribution of black pigment spots (probably photophores) shows the close relationships between these genera. This character may prove very useful when more ultrastructual information becomes available for other squalomorphs.

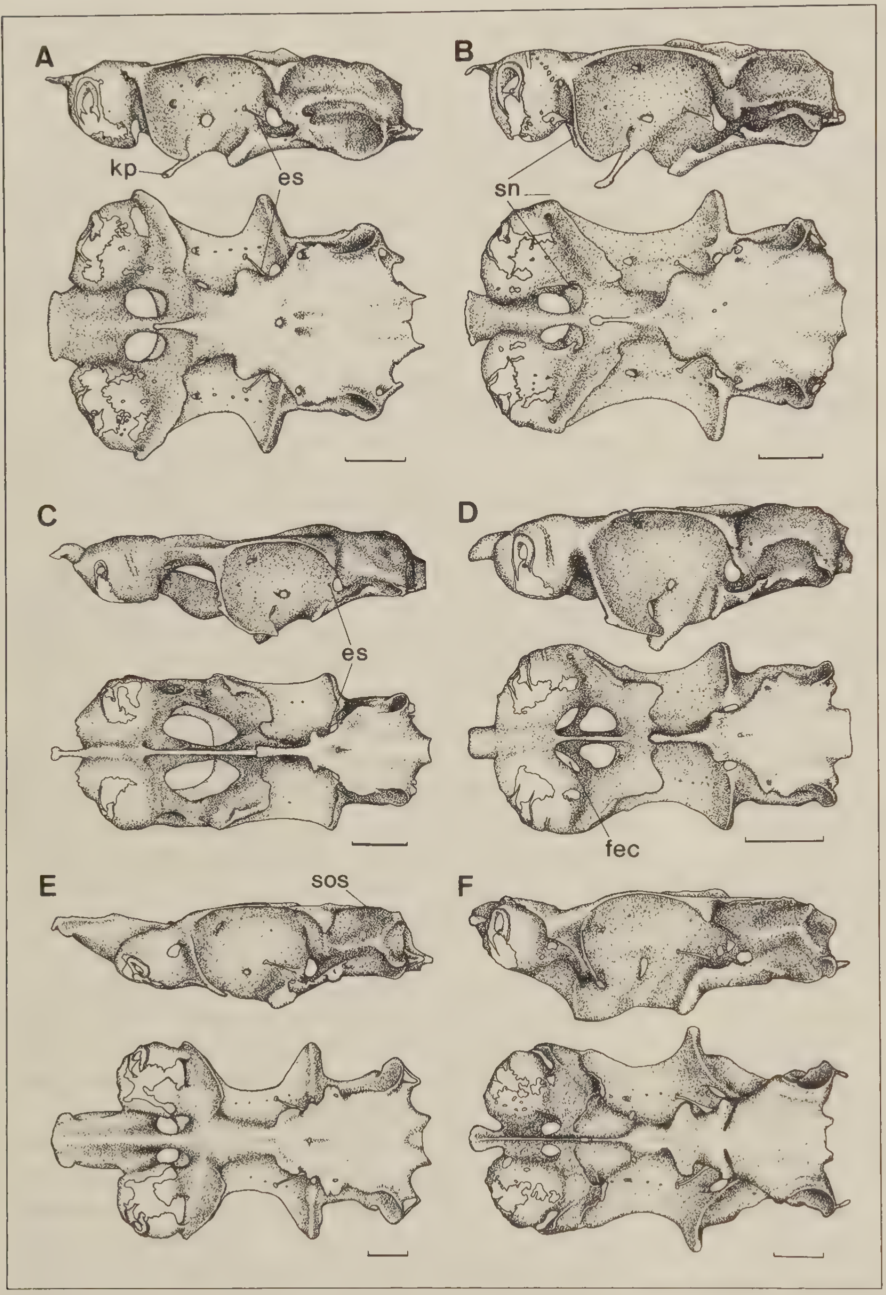

Figure 2.
Lateral (above) and ventral (below) aspects of neurocrania. A, *Aculeola nigra*; B, *Centroscyllium ritteri*; C, *Miroscyllium sheikoi*; D, *Etmopterus lucifer*; E, *Squalus mitsukurii*; F, *Zameus squamulosus*. es = eye stalk; fec = fenestra at anterior wall of ectethmoid chamber; kp = keel-process of basis cranii; sn = subnasal stay; sos = supraotic shelf. Scale bars indicate 10 mm.

Interrelationships of Etmopterinae

Eleven morphological differences for character analysis are recognized within the subfamily Etmopterinae, and are briefly described below. In each, the derived state is mentioned first and the plesiomorphy is shown in brackets. The conditions of other squalomorphs are also described.

Neurocranium (Fig. 2)—(5) In *Etmopterus*, the nasal capsule uniquely has a relatively large fenestra (fec) piercing the ectethmoid chamber [absent in other etmopterine genera and other squalomorphs]. (6) All *Centroscyllium* (except *C. sheikoi*) possess a simple rod-like process (sn) extending ventrally at outer margin of subnasal fenestra, which is called a ''subnasal stay'' in this study [absent in all other squalomorphs]. (7) *C. sheikoi* has a wide interspace between nasal capsule and the antorbital wall [very narrowly spaced in all other etmopterines]. In most squalomorphs, the nasal capsule is close to or almost unified with the antorbital wall. The elongation between them is notably developed in *Deania* and is also observed in *Centroscymnus crepidater*. (8) The eye stalk (es) is a short rod-like process, not chondrified distally, in *Etmopterus*, *C. nigrum*, and *C. sheikoi* [it is a long and slender process with a disc at its extreme point in other etmopterine species]. The former

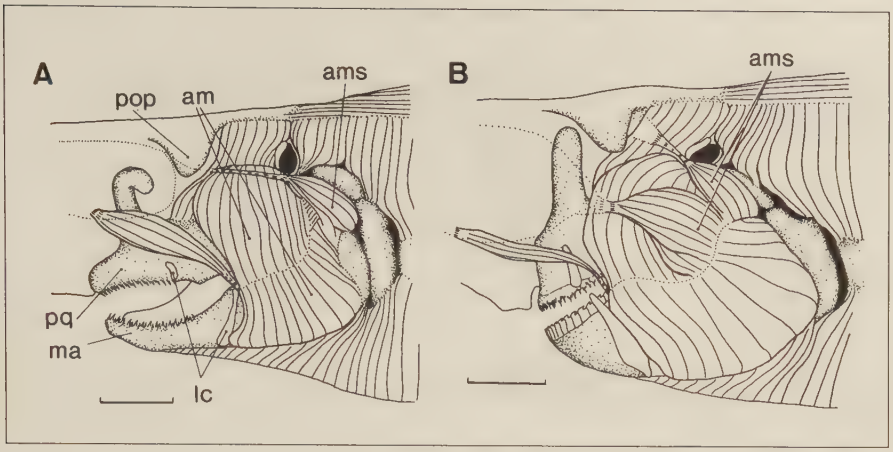

Figure 3.
Lateral aspect of head muscles. A, *Aculeola nigra*; B, *Etmopterus spinax*. am = adductor mandibulae; ams = adductor mandibulae superficialis; lc = labial cartilages; ma = mandibula; pop = postorbital process; pq = palatoquadrate. Scale bars indicate 10 mm.

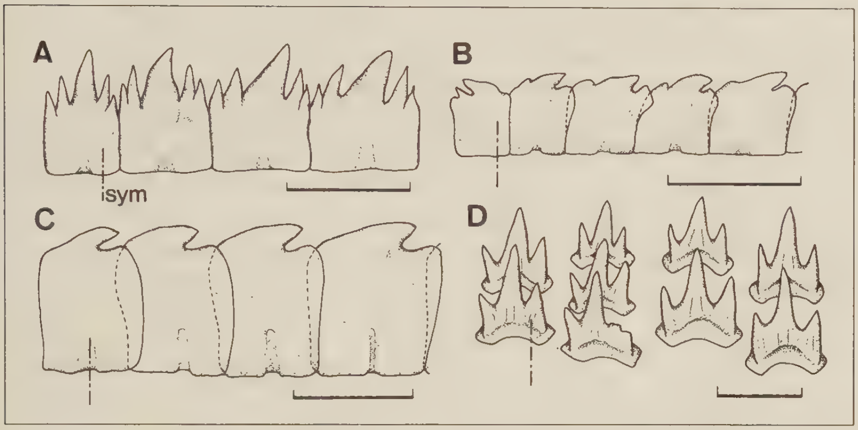

Figure 4.
Frontal aspect of anterior lower jaw teeth. A, *Miroscyllium sheikoi* (adult male: HUMZ 74982); B, *M. sheikoi* (young male: HUMZ 74984); C, *Etmopterus spinax* (SU 20617); D, *Centroscyllium ritteri* (HUMZ 93929). sym = jaw symphysis. Scale bars indicate 1 mm.

condition for the eye stalk is also observed in the genera *Deania* and *Oxynotus*, and the latter is found in all other squalomorphs except for *Isistius*, which does not have any process to support the eye and rectus muscles.

Visceral Arches and Related Parts—(9) Lower jaw teeth interlock their neighbors to form a continuous serrated edge in *Etmopterus* and *Centroscyllium sheikoi*: the overlapping condition of *C. sheikoi* occurs only in younger stages, and are normally lost with growth [teeth neither interlock nor touch their neighbors in all the other etmopterines] (Fig. 4). The interlocking of lower jaw teeth is observed in all of the other squalids. In hexanchoids and echinorhinids, they are arranged along the jaw but separated from the neighbors, and in pristiophoriforms, teeth are arranged quincuncially as are those of *Centroscyllium* and *Aculeola*. *Chlamydoselachus* has a unique dentition among living species. Its lower jaw teeth form many transverse rows widely separated from their neighbors. (10) In *E. baxteri*, *E. schultzi*, *E. spinax*, *E. unicolor*, and *E. virens*, the adductor mandibulae superficialis (ams) is divided into anteroventral and posterodorsal portions [only the latter is present in other squalomorphs] (Fig. 3). (11) The geniocoracoideus (gco) has its origin on the ventral surface of the symphysis of the coracoid cartilages (co) in *Centroscyllium* and *Aculeola* [from the septum that is formed by the rectus cervicis (rc) and the pericardial membrane in *Etmopterus*]. The former condition for this muscle also occurs in *Dalatias* and *Zameus*, and the latter condition is seen in all other squalid genera except *Isistius*, in which the geniocoracoideus originates from the surface of the continuous muscle mass from the voluminous rectus cervicis and ventral longitudinal bundle. In echinorhinids, pristio-phoriforms, and hexanchiforms, the geniocoracoideus originates on the aponeurotic septum which is formed by anterior and posterior portions of rectus cervicis (Fig. 5). (12) In *Aculeola*, the basihyal cartilage (bh) has a double-pointed expansion (dp) at its rear margin [absent in other squalomorphs] (Fig. 6A).

Other Parts—(13) *Aculeola* also possesses a double-pointed expansion (dp) at the anterior edge of the puboischiadic bar (pb) [absent in other squalomorphs] (Fig. 6B). (14) In *Etmopterus* and *Centroscyllium sheikoi*, the transformation from monospondylous to diplospondylous vertebral centra occurs well behind the haemal canal origin, and the most anterior five to nine precaudal tail centra are monospondylous [generally, such extensive monospondyly is not observed in the precaudal tail centra of other squalomorphs]

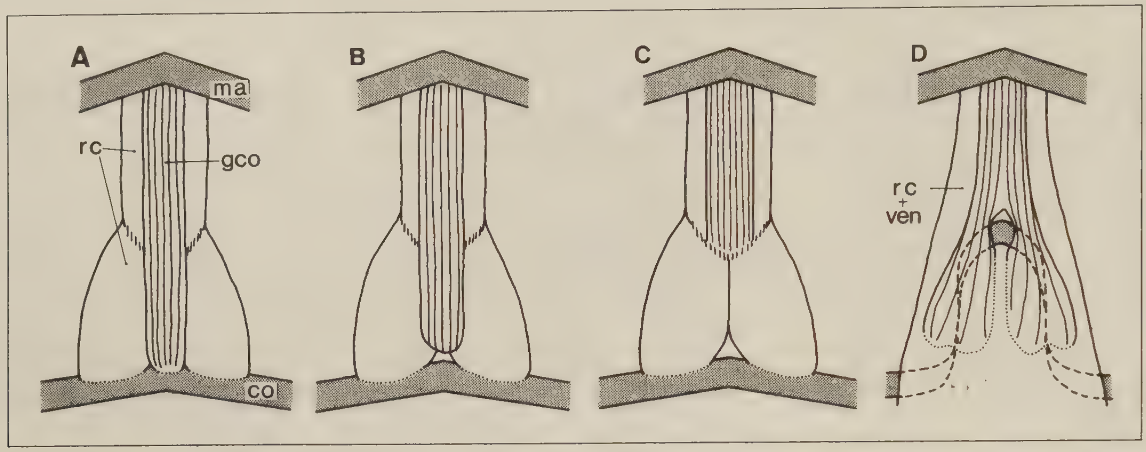

Figure 5.
Diagrams of ventral surface of head muscles, showing the four patterns of origin of geniocoracoideus. Geniocoracoideus originates from: A, ventral surface of coracoid; B, septum of rectus cervicus and pericardial membrane; C, aponeurotic septum of anterior and posterior portions of rectus cervicis; D, ventral surface of a continuous muscle mass from rectus cervicis and ventral longitudinal bundle. co = coracoid; gco = geniocoracoideus; ma = mandibula; rc = rectus cervicis; ven = ventral longitudinal bundle.

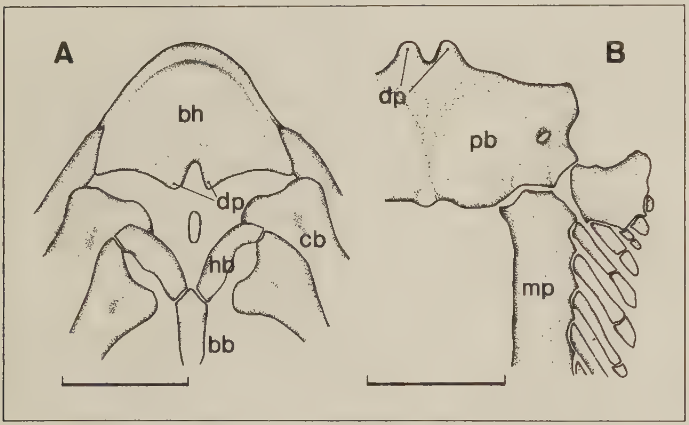

Figure 6.
Unique double-pointed expansions of *Aculeola nigra*. A, dorsal aspect of basal component of hyoid and branchial arches (anterior part); B, ventral aspect of pelvic girdle. bb = basibranchial; bh = basihyal; cb = ceratobranchial; dp = double-pointed expansion; hb = hypobranchial; mp = metapterygium; pb = puboischiadic bar. Scale bars indicate 10 mm.

(Fig. 7). (15) The dermal denticles are almost absent on the body surface in *C. kamoharai* [the distribution of denticles is more or less described on the bodies of other squalomorphs].

The most parsimonious hypothesis of etmopterine relationships is shown in Fig. 8. The Etmopterinae is inferred to be composed of two major phyletic lines. The first line is monophyletic by virtue of synapomorphy (11) and has two branches corresponding to genera *Aculeola* and *Centroscyllium* (except *C. sheikoi*). These results support the view of Burgess and Springer (1986), who recognized the close relationship between the two genera based on oral structures and dermal denticles. The genus *Aculeola* is monotypic (*A. nigra*) and is defined by two apomorphies, (12) and (13). As suggested by Compagno (1973), Maisey (1980) and Burgess and Springer (1986), it is concluded that *Aculeola* is the least specialized genus within the Squalidae because it shares some symplesiomorphies with echinorhinids or hexanchiforms, i.e., a long palatoquadrate without developed otic process, "amphystylic" jaw protrusion as hexanchoids (but, no postorbital articulation), coracoid cartilages extending extremely forward, comparatively broad pelvic girdle and no calcified vertebral centra. The *Centroscyllium* branch is considered monophyletic by virtue of synapomorphy (6). The interspecific relationships of the genus *Centroscyllium* remains obscure in this study, because we find only two autapomorphies exhibited by both *C. kamoharai* and *C. nigrum* and no shared derived condition (synapomorphy) in the group. We also cannot address the validity of *Paracentroscyllium* Alcock (1889), proposed for *C. ornatum* and revived by Fowler (1941) as a subgenus of *Centroscyllium*, because we have not examined the appropriate specimens. External and internal morphology of *Centroscyllium* species are so conservative that this genus (except *C. sheikoi*) is considered to form a well defined unit.

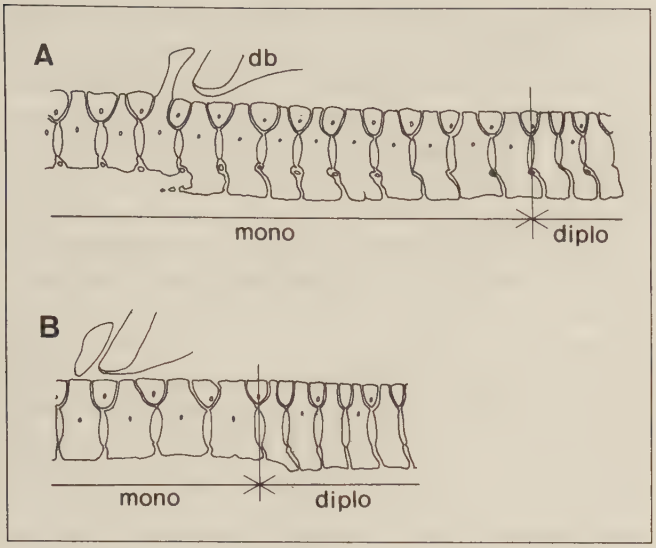

Figure 7.
Diagrams showing the transformation from monospondyly to diplospondyly under 2nd dorsal fin. A, *Miroscyllium sheikoi*; B, *Centroscyllium ritteri*. db = basal cartilage of 2nd dorsal fin; diplo = diplospondylous centra; mono = monospondylous centra.

The second phyletic line also consists of a pair of sister groups which correspond to the genus *Etmopterus* and *Centroscyllium sheikoi*. The close relations between these two groups are supported by the synapomorphies (8), (9), and (14). *Etmopterus* forms a monophyletic group by virtue of (5), and is the most varied genus (over 20 nominal species) in the Etmopterinae. In this genus, *E. baxteri*, schultzi, *spinax*, *virens*, and *unicolor* are united by an autapomorphic character (10). These five species also characterized by having spine-like dermal denticles spaced randomly in adult forms. The remaining members of the *Etmopterus* do not share any derived character states. This hypothesis of *Etmopterus* interrelationships eliminates Fowler's (1941) subgenera, *Etmopterus* and *Acanthidium*, which are proposed on the relative positions of pectoral, pelvic, and two dorsal fins. The last group contains *Centroscyllium sheikoi* (= *Miroscyllium sheikoi*), which is defined by the synapomorphies (7) and (11). This species was originally described as a species of *Centroscyllium* based on a mature male specimen from Kyushu-Palau Ridge (Dolganov 1986). It corresponds to species tentatively reported by Nakaya (1982) as *Centroscyllium* sp. (adult males) and Etmopterus sp. (young males). Its lower jaw tooth is blade-like and touches it's neighbors in adult males, whereas in young

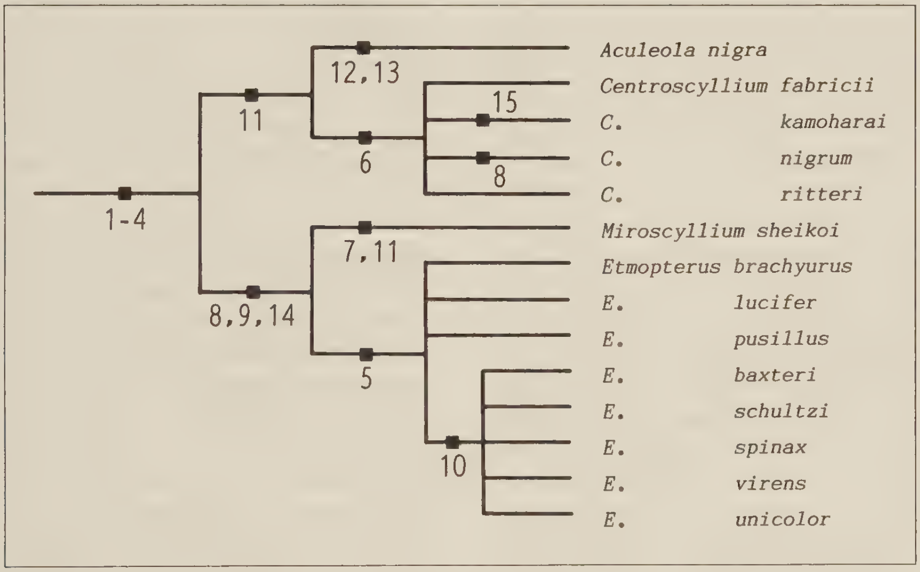

Figure 8.
Propossed interrelationships of the subfamily Etmopterinae. Numbers in the figure showing following apomorphies: 1, keel-process of basal cranii present; 2, labial cartilages composed of two separated parts; 3, supraotic shelf absent; 4, prespinal radial present; 5, fenestra at anterior wall of ectethmoid chamber present; 6, subnasal stay present; 7, wide interspace between nasal capsule and antorbital wall; 8, eye stalk not chondrified distally; 9, lower jaw teeth interlocking; 10, adductor mandibulae superficialis divided into two parts; 11, geniocoracoideus immediately originating from ventral surface of coracoid; 12, double-pointed expansion at rear margin of basihyal present; 13, double-pointed expansion at anterior margin of puboischiadic bar; 14, most anterior five to nine precaudal tail centra monospondylous; 15, dermal denticles almost absent on body.

males it is monocuspid (one or two minute lateral cusps in some teeth) and interlocking like that of *Etmopterus*. This morphological change is considered to occur with growth, and we are very interested in observing the female dentition of *Etmopterus*.

Taxonomic Conclusions

The present phylogenetic study expressed the monophyly of the Etmopterinae and the presence of four equally ranked taxa in the group. Of these supraspecific taxa, all the *Etmopterus species* + *Centroscyllium sheikoi*, and the rest of the *Centroscyllium* + *Aculeola* are the sister groups. These findings necessitate that *C. sheikoi* be excluded from the genus *Centroscyllium*, and that it be raised to the generic rank. We propose the new genus name, *Miroscyllium*, for the taxon.

Diagnostic characters of each taxa are described below.

Subfamily Etmopterinae

Diagnosis—Both dorsal fins with a grooved spine, the second relatively larger; caudal fin with a long upper margin and a subterminal notch; neither abdominal ridge, precaudal ridge nor precaudal pits present; mouth with thin lips and labial furrows, lips not fringed; upper jaw teeth with a conical and slender central cusp rising from bilobed and semihexagonal bases, arranged quincuncially; minute to prominent lateral cusps present in almost all of the species (recognized even in the genus *Aculeola*: Burgess and Springer, 1986: our USNM specimen of this study); keel-process of basis cranii present; two labial cartilages on the mouth corner developed; supraotic shelf absent; prespinal radials of second dorsal fin more or less developed.

Other Features—Precerebral fontanelle large and oval; ectethmoid chamber developed, and subnasal fenestra present; antorbital wall large, with a membranous part below the eye; foramen prooticum for trigeminal and facial nerve (except hyomandibular branch) single; posterior part of palatobasal process moderately expanded laterally; short subotic shelf in front of articular fossa for hyomandibula. Palatoquadrate large, consisting of only a single thick plate, with a long orbital process and no symphysial plate; suborbitalis inserted on inner side of labials (and its adjacent tissues) and on the anteroventral part of adductor mandibulae by a short tendon, not directly inserted on mandibula; second and third hypobranchials of both sides not fused; subspinalis muscle present. Pectoral fin skeletons including three basal cartilages and radials; iliac process of pelvic girdle weakly developed. Each dorsal fin with a triangular basal cartilage but lacks three jointed rays; postspinal rays are moderately elongated.

Genus *Etmopterus* Rafinesque

Diagnosis—Upper jaw teeth with one to five pairs of lateral cusps; lower jaw teeth, dissimilar to the uppers in shape, with blade-like and single oblique cusp, arranged linearly along the jaw and overlapping the neighboring teeth; fenestra at anterior wall of ectethmoid chamber piercing the nasal capsule; eye stalk short, not chondrified distally, without a disk at the extreme point; anterior several vertebral centra of the precaudal tail monospondylous.

Other Features—Snout moderately rounded, not elongated, with a more or less wedge-shaped tip; oral cleft relatively short and transverse; dermal denticles with a slender, acute and erect to weakly inclined thorn-like, bristle-like, or flat truncated cusp, spaced relatively close together, forming longitudinal rows in some species; flank marks at caudal region conspicuous or almost absent. Rostral process short, simple and club-like, separable from precerebral fontanelle; keel-process rather thick. Mandibular arch rather short; palatoquadrate with laterally expanded otic process for adductor mandibulae; adductor mandibulae superficialis divided into two portions in some species; geniocoracoideus having its origin from an aponeurotic septum that is formed by the rectus cervicis and pericardial membrane.

Genus *Centroscyllium* Müller and Henle

Diagnosis—Upper and lower jaw teeth similar in shape and quincunx arrangement, with one to two pairs of minute but prominent lateral cusps; subnasal stay at outer margin of subnasal fenestra; geniocoracoideus having its origin from the ventral surface of the midline of the coracoid.

Other Features—Snout moderately rounded to slightly pointed; oral cleft relatively long and arcuate; dermal denticles with a short, slender, acute or blunt, erect to weakly inclined cusp, spaced very sparsely and randomly, or almost naked; flank marks at the caudal region conspicuous or absent. Rostral process thin, plate-like, forming the anterior edge of precerebral fontanelle, not supported ventrally; keel-process comparatively slender. Mandibular arch rather long; palatoquadrate with otic process; adductor mandibulae superficialis consisting of only posterodorsal portion; trunk centra monospondylous, and precaudal tail centra diplospondylous in many specimens.

Genus *Aculeola* de Buen

Diagnosis—Upper jaw teeth similar to the lower in shape and arrangement, without lateral cusps or with very minute ones in some specimens; dorsal fin spines relatively slender, not curved strongly, not reaching halfway to the fin apex; geniocoracoideus having its origin from the ventral surface of the midline of the coracoid bar; double-pointed expansions at the posterior edge of the basihyal and at the frontal edge of the puboischiadic bar.

Other Features—Snout short; oral cleft relatively long and arcuate; dermal denticles with a short, nearly erect and conical cusp, spaced sparsely and randomly; no flank marks at the caudal region. Rostral process thin, plate-like, forming the anterior edge of precerebral fontanelle; keel-process comparatively slender. Mandibular arch rather long; palatoquadrate without otic process for adductor mandibulae; palatoquadrate almost in contact with the rear margin of the postorbital process (Maisey 1980); adductor mandibulae superficialis consisting of only posterodorsal portion. Coracoid cartilage relatively thick, extending forward at ventral surface of body, forming wedge-shaped bar; vertebral centra poorly developed, uncalcified; trunk centra monospondylous and precaudal tail centra diplospondylous.

***Miroscyllium* gen. nov.**

Type species. *Centroscyllium sheikoi* Dolganov, 1986.
Synonymy. *Centroscyllium* (in part) Nakaya, 1982.
Etmopterus (in part) Nakaya, 1982.

Diagnosis—A slender-bodied etmopterine shark with a long snout and relatively short trunk; lower jaw teeth blade-like with one central and several short lateral cusps (in the adult male; the latter are sometimes absent in younger males), touching (in adult male) or overlapping (in young male) neighboring teeth. One or more functional tooth series in both jaws: eye stalk short, not chondrified distally, without a cartilaginous disk supporting the eye ball; recti anterior, superior, and inferior, having origins at the proximal part of eye stalk; geniocoracoideus originating directly from the ventral surface of the symphysis of coracoid cartilages; transformation from monospondylous to diplospondylous centra well behind the haemal canal origin; there are about nine monospondylous centra in the precaudal tail.

External—Snout relatively elongated and flattened, with a wedge-shaped tip; oral cleft relatively short and transverse; upper jaw teeth with a central cusp and two to four pairs of lateral cusps (sometimes two prominent cusps can be observed), arranged quincuncially; lower jaw teeth in adult males small and blade-like with a multicuspid crown, arranged linearly along the jaw, not overlapping but touching their neighbors to form a serrated edge; in young males, lower teeth with an inclined main cusp, with or without 1 or 2 minute lateral cusps, and interlocking as seen in *Etmopterus* species (Fig. 4A, B). Dorsal fin spines strong, relatively curved posteriorly, the second strikingly larger than the first, extending nearly to the apex of the fin; upper and lower caudal lobes are poorly developed. Dermal denticles are very flat, truncated at the top, spaced relatively close together and in random order; flank marks at the caudal region conspicuous.

Internal—Rostral process rather long, simple, and club-like, separable from precerebral fontanelle; subethmoid ridge comparatively well developed; interspace between nasal capsule and antorbital wall moderately elongated; keel-process comparatively thick. Mandibular arch rather short; palatoquadrate with otic process and long orbital process; palatoquadrate not in contact with rear margin of postorbital process; the anteroventral portion of the adductor mandibulae superficialis absent. Coracoid cartilage rather slender, not extending forward at ventral surface of body, forming a moderately curved bar; pelvic girdle relatively narrow, moderately curved. Vertebral central with a calcified double cone.

Etymology—From the Latin *mir* (strange) in reference to the unique tooth series on the lower jaw.

Remarks—Only a few adult and young male specimens of *Miroscyllium sheikoi* have been captured from Kyushu-Palau Ridges, western North Pacific.

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Relationships of the Megamouth Shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), with Comments on Its Feeding Habits

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ABSTRACT

The hypothesis that the megamouth shark (*Megachasma pelagios*, order Lamniformes, family Megachasmidae) is a cetorhinid is rejected by phenetic and cladistic analyses. A phenetic list of characters separating *Megachasma* and *Cetorhinus* is presented. A cladistic analysis of the Lamniformes rejects the hypotheses that *Megachasma* is the sister group of *Cetorhinus* or that *Megachasma* is the primitive sister of all other lamnoids. The Megachasmidae is the primitive sister group to the Alopiidae, Cetorhinidae, and Lamnidae; the Cetorhinidae is sister to the Lamnidae; and the Alopiidae to the Lamnidae and Cetorhinidae. *Mitsukurina* may be the primitive sister group of all other lamnoids, but relationships of other lamnoids with aplesodic pectoral fins is uncertain. The Alopiidae are monophyletic, with *Alopias vulpinus* the primitive sister species of *A. pelagicus* and *A. superciliosus*. The Lamnidae are also monophyletic, but the arrangement of *Lamna* as the sister genus of *Carcharodon* and *Isurus* requires confirmation. Some Cenozoic fossil shark teeth, including *Megascyliorhinus*, may be megachasmids but tentatively fall in their own genus or genera. The Cretaceous *Squalicorax* has some derived cranial features in common with *Megachasma* but otherwise is very different and probably had a macropredatory life-history style. The megamouth shark probably does not passively filter its food while swimming as does the basking shark; it probably expands its buccal cavity and sucks its prey into its mouth. This would be more efficient if the mouth of this shark was luminescent and attracted prey.

Introduction

On 15 November 1976, a U.S. Navy research vessel working off Oahu, Hawaii caught a 750 kg, 446 cm long adult male shark of bizarre and unusual form (Fig. 1A) in a parachute sea anchor and brought it to port despite its flabby bulk. The first ''megamouth shark'', as it was soon dubbed by the press because of its enormous mouth and jaws, was frozen and preserved intact and is now housed in the Bernice P. Bishop Museum (BPBM), Honolulu, Oahu, Hawaii. On 29 November 1984, a second adult male megamouth shark, 449 cm long and weighing ~705 kg, was captured in a pelagic gill net by a commercial fishing boat off Catalina Island, California and preserved intact in the Natural History Museum of Los Angeles County (LACM) (Lavenberg and Seigel 1985). On 18 August 1988, a third megamouth shark, an adult male 515 cm long and weighing ~690 kg, washed up alive on a beach at Mandurah, near Freemantle, Western Australia and was collected and preserved intact by the Western Australian Museum (G. R. Allen and N. Haigh, Western Australian Museum, Perth, Australia, pers. commun., 1988).

Taylor et al. (1983) described the megamouth shark as *Megachasma pelagios* in the monotypic family Megachasmidae (order Lamniformes, lamnoid sharks). Taylor et al. gave definitions of *Megachasma pelagios* and the Megachasmidae and compared the Megachasmidae with other lamnoid families. Lamnoid derived characters of the Megachasmidae include its elongated ring intestinal valve, reduction of basal ledges and grooves on its teeth, possibly its osteodont tooth histotype (Compagno 1988), absence of subocular ridges, reduced labial cartilages, and vertebral calcification pattern.

Taylor et al. (1983) noted that the megamouth shark shared derived plesodic pectoral fins with the advanced lamnoid families Alopiidae, Cetorhinidae, and Lamnidae and had teeth that are superficially similar to those of the only other lamnoid filter feeder, the basking shark

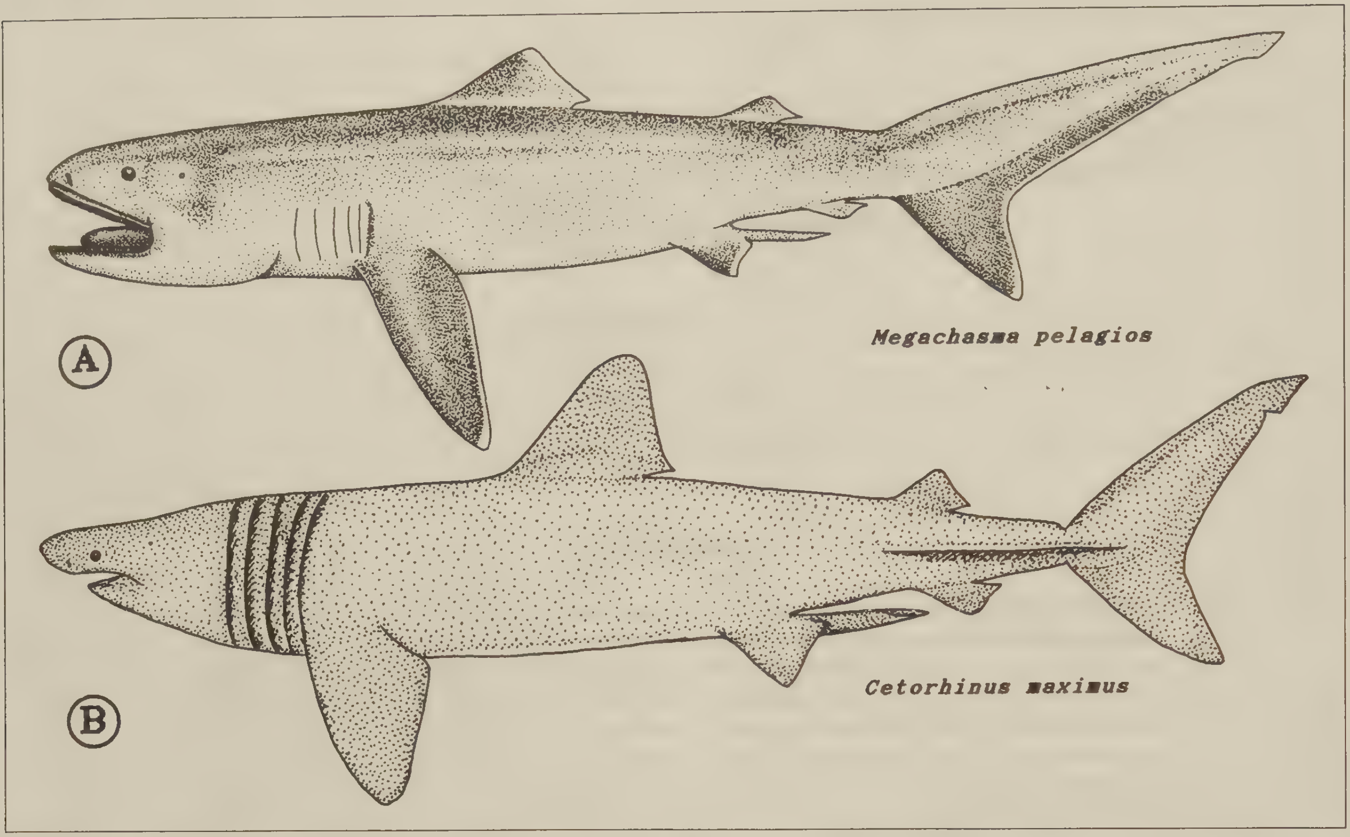


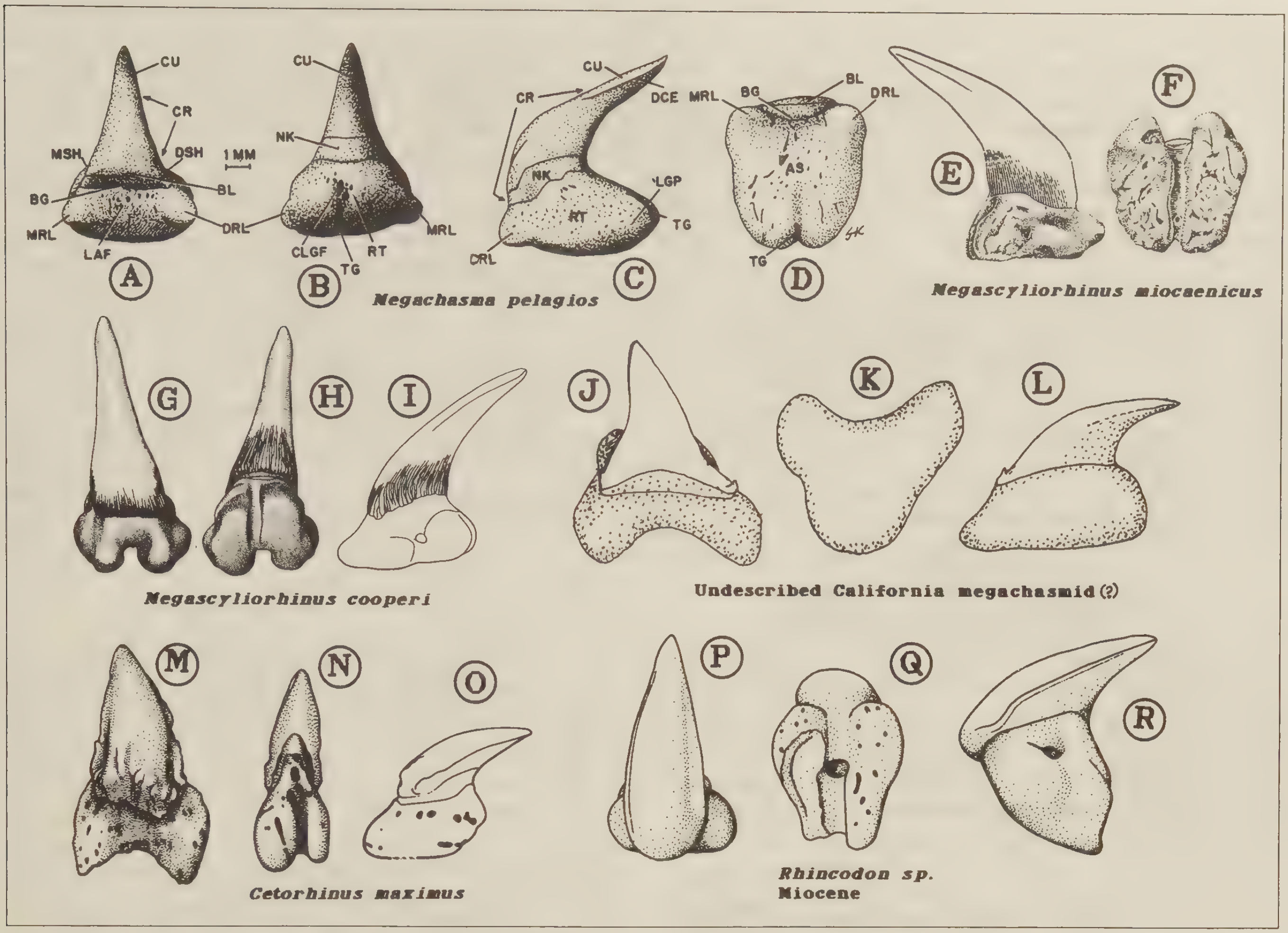
Figure 1.
A, Megamouth shark, *Megachasma pelagios* Taylor, Compagno and Struhsaker, 1983, based on the holotype (BPBM-22730, 4460 mm adult male), from Compagno (1984). B, Basking shark, *Cetorhinus maximus* (Gunnerus, 1765), original drawing based on LACM-35593-1 (7010 mm adult male).

(*Cetorhinus maximus*, family Cetorhinidae). Taylor et al. suggested, as an alternative to placing megachasmids with the advanced lamnoids, that the Megachasmidae might be the primitive sister group of all other living lamnoids. This was based on the presence of strong palatoquadrate orbital processes and the absence of differentiated tooth row groups in *Megachasma pelagios*, which was thought at the time to be primitive relative to other lamnoids. However, Taylor et al. suggested that the simple dentition of the megamouth shark might be secondarily reduced, correlated with its functional replacement by gill rakers.

Maisey (1985) rejected the placement of *Megachasma* as the sister-group of all other lamnoids but was convinced that plesodic pectorals united *Megachasma* with the advanced lamnoid families. He suggested that the megamouth shark was confamilial with the basking shark (Fig. 1B) because of synapomorphies in their jaw suspension, cranial morphology, dentition, and filter-feeding structures. Maisey (1985) stated that *Cetorhinus* and *Megachasma* ''seem to form a monophyletic group of specialized filter-feeding lamniforms.''

Fossil shark teeth similar to those of the living megamouth shark (Fig. 2J–L) were known from early Miocene deposits of the southern San Joaquin Valley of California since the 1960s (S. P. Applegate, Instituto de Geologia, Universidad Nacional Autonoma de Mexico, Mexico City, Mexico, pers. commun., 1970). These common fossils were difficult to place, and paleontologists and neontologists disagreed as to whether they were primitive carcharhinoid sharks (Scyliorhinidae or Pseudotriakidae) or noncarcharhinoid sharks. Apart from external differences, these teeth have an osteodont histotype unlike the orthodont type of primitive carcharhinoids (see Compagno 1973b, 1988). Similar teeth were subsequently found in the late Oligocene or early Miocene of northern California and central Oregon, Phillips et al. (1976) (B. J. Welton, Chevron Oil Field Research Co., Bakersfield, California, pers. commun., 1983). After the capture of the first megamouth shark and comparison of its teeth with these fossils, it seemed likely that the fossils were megachasmids.

Cappetta and Ward (1977) described *Megascyliorhinus* as a fossil catshark (Carcharhiniformes: Scyliorhinidae), based on *M. cooperi* Cappetta and Ward, 1977 (Fig. 2G–I) from Eocene London Clay. Previously Antunes and Jonet (1970) had described *Rhincodon miocaenicus*, a supposed fossil whale shark (Fig. 2E–F), from the Miocene of Portugal, but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Megascyliorhinus miocaenicus
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Megascyliorhinus cooperi
Undescribed California megachasmid (?)
M
N
O
Cetorhinus maximus
P
Q
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Rhincodon sp.
Miocene

Figure 2.

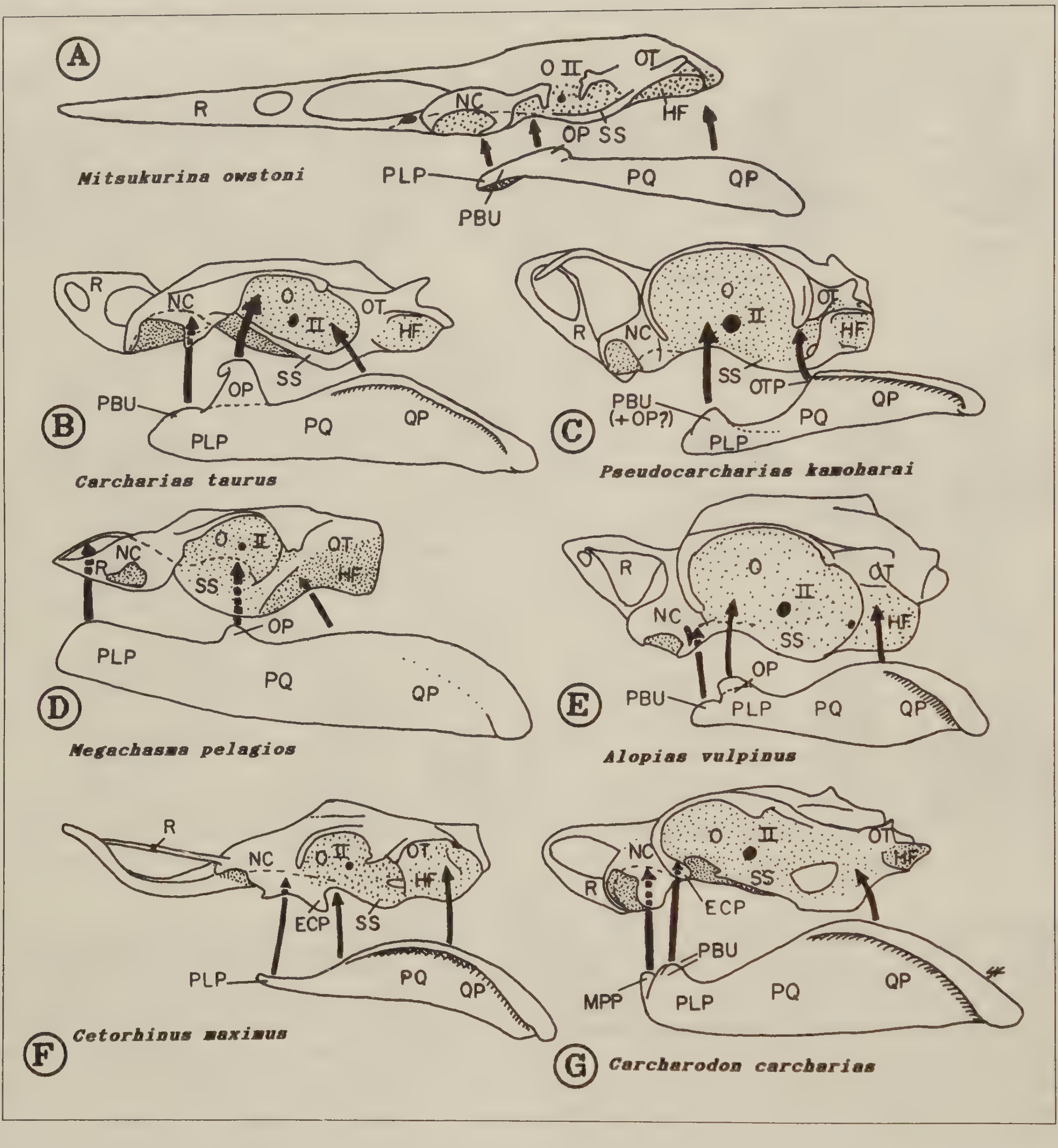
Teeth of megachasmids and other sharks with reduced roots and crowns. A–D, *Megachasma pelagios*, tooth of BPBM-22730 in A, labial; B, lingual; C, lateral; and D, basal views, after Taylor et al. (1983). E–F, *Megascyliorhinus miocaenicus* (Antunes and Jonet, 1970), tooth of the holotype in E, lateral and F, basal view, after Antunes and Jonet (1970). G–I, *Megascyliorhinus cooperi* Cappetta and Ward, 1977, tooth of the holotype in G, labial; H, lingual; and I, lateral views, after Cappetta (1987). J–L, Undescribed megachasmidlike teeth (LACM-VP-10353, Jewett Sand, Pyramid Hill, Kern Co., California, Miocene, Arikareean), original, in J, labial; K, basal; and L, lateral views. M–O, *Cetorhinus maximus*, teech in M, labial; N, basal; and O, lateral views, from Cappetta (1987). P–R, *Rhincodon* sp. from Miocene of France, tooth in P, labial; Q, basal; and R, lateral views, from Cappetta (1987).

Cappetta and Ward transferred it to the Scyliorhinidae and to their genus *Megascyliorhinus*. Cappetta (1987) noted several additional records of *Megascyliorhinus* species from the Lower Eocene to the Pleistocene of Europe, Africa, Australia, New Zealand, South America, and Japan. Cappetta retained *Megascyliorhinus* in the Scyliorhinidae, but noted that this genus has osteodont teeth and may not be a scyliorhinid or a member of the order Carcharhiniformes. Some paleontologists (D. A. Ward, University of London, London, England, pers. commun., 1979; F. J. Pfeil, Pfeil Verlag, Munich, West Germany, pers. commun., 1986) have suggested that *Megascyliorhinus* is a megachasmid and that *Megachasma* may even be a synonym of *Megascyliorhinus*.

This paper reviews the relationships of the megamouth shark to the basking shark and other living lamnoids, and to possible fossil relatives. In addition, the scenario for megamouth feeding presented by Taylor et al. (1983) is reconsidered and modified with further morphological evidence from two of the three specimens of *Megachasma pelagios*.

Taxonomic Characters and Terminology

The taxonomic characters used here are primarily derived from the specimens listed below (see Appendix: Comparative Material of Lamnoid Taxa). The works of Pavesi (1874, 1878), Haswell (1885), Parker (1887), Jordan (1898), Jungersen (1899), Garman (1913), Ridewood (1921), Senna (1925), White (1937), Matthews (1950),


A
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Mitsukurina owstoni
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OP
PBU
PLP
PQ
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Carcharias taurus
C
R
NC
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HF
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PBU (+OP?)
PLP
PQ
QP
Pseudocarcharias kamoharai
D
R
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II
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Megachasma pelagios
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Carcharodon carcharias

Matthews and Parker (1950), Springer and Garrick (1964), Parker and Stott (1965), and Branstetter and McEachran (1986) were of particular use in supplementing specimens.

Jaw morphology and suspension in lamnoids (Fig. 3) is more variable than in other sharks and shows a number of derived states beyond the primitive type in Alopiidae and Odontaspididae. These have palatoquadrates with large orbital processes (OP) articulating in the orbital notches of the orbit as in carcharhinoids, and large dental bullae that articulate with the subethmoid fossa of the chondrocranium. The derived types are discussed in Compagno (1988) and below. The term "orbital process" is not restricted to dorsomesial articular projections of the palatoquadrate palatine processes in squalomorph and squatinomorph sharks only, as proposed by Maisey (1980, 1985). Orbital processes also include similar processes on the palatoquadrates of some lamnoids and other galeomorph sharks (Compagno 1988).

The chondrocranium of living lamnoids (Figs. 4–7) was especially useful for elucidating the interrelationships of lamnoids. A detailed account of lamnoid cranial morphology is beyond the scope of this account, but will be presented elsewhere.

Lamnoids fall into two groups on the structure of the pectoral fin skeleton. Those genera with aplesodic pectoral fins have the distal radials not extending into the fin web,

Figure 3.
Diagram of jaw suspension types of living lamnoids, and showing cranial-palatoquadrate articulations. A, *Mitsukurina owstoni*, based mostly on RUSI-6206, 1166 mm immature female; derived type in Mitsukurinidae with elongated dental bullae of palatine processes fitting in subethmoid fossa between nasal capsules and slung from orbital notches by loose ethmopalatine ligaments attached to orbital processes. B, *Carcharias taurus*, from CAS 1961-IX:21, 1540 mm immature female; primitive type in Odontaspididae with large dental bullae articulating with subethmoid fossa and with large, semicartilaginous orbital processes articulating with orbital notches. C, *Pseudocarcharias kamoharai*, from LACM-uncat., 1100 mm adult male; derived type in Pseudocarchariidae with dental bullae and orbital processes apparently coalesced, bullae fitting in orbital notches rather than subethmoid fossa, and quadrate processes articulating with postorbital processes. D, *Megachasma pelagios*, from BPBM-22730, 4460 mm adult male; derived type in Megachasmidae with enlarged palatine processes fitting under rostrum, orbital processes fitting in deep, pits in basal plate, and suborbital shelves fitting laterally over palatoquadrates. E, *Alopias vulpinus*, from LJVC-0382, 1605 mm immature female; primitive type in Alopiidae essentially as in Odontaspididae except for reduced jaws. F, *Cetorhinus maximus*, based in part on Maisey (1985), but with cranium modified after LACM-35593-1 and LACM-42649-1; derived type in Cetorhinidae with orbital processes and dental bullae lost and with palatine processes fitting into subethmoid fossa and extending through orbital notches; palatoquadrate movement limited anteriorly by expanded ectethmoid processes, posteriorly by lateral wings of suborbital shelves. G, *Carcharodon carcharias*, from LJVC-0384, 1990 mm immature female; derived type in Lamnidae with no orbital processes, dental bullae and unique mesial processes articulating with subethmoid fossa; ectethmoid processes restrict movement of palatoquadrates anteriorly, lateral wings of suborbital shelves posteriorly.
ABBREVIATIONS: II = foramen for optic nerve; HF = hyomandibular facet; MPP = mesial process at symphysis of palatoquadrates (unique to Lamnidae); NC = nasal capsule; OP = orbital process; OT = otic capsule; PBU = dental bulla of palatine process; PLP = palatine process; PQ = palatoquadrate; QP = quadrate process; R = rostrum; SS = suborbital shelf.

while those with plesodic pectorals have these radials greatly elongated and supporting the fin web. Aplesodic pectoral fins are primitive and plesodic pectorals are derived in living sharks (Compagno 1988).

All living lamnoids have elongated ring intestinal valves (White 1937) with over 15 turns to the valve, which are derived relative to other shark groups. Some lamnoids are further derived in having counts well beyond the 19–30 found in the primitive lamnoids *Mitsukurina* and *Carcharias*. A frequency distribution of valve counts for living lamnoids (Fig. 8) indicates that more derived taxa usually have higher counts.

Several character systems of use in lamnoid systematics, including the hyobranchial skeleton, fin skeletons, clasper morphology, vertebral numbers and ratios, mode of reproduction, and brain morphology are unknown or inadequately known in the megamouth shark and some other lamnoids. These require further investigation and are not included in the analyses here.

Terminology for lamnoid morphology and methodology for its study follows Compagno (1970, 1973a, b, 1979, 1984, 1988) and Taylor et al. (1983). Lamnoid systematics and nomenclature follows Compagno (1984) with one exception. A recent ruling of the International Commission on Zoological Nomenclature (Opinion 1459, 1987) has reinstated the genus *Carcharias* Rafinesque, 1810, which is used here in place of *Eugomphodus* for *C. taurus*.

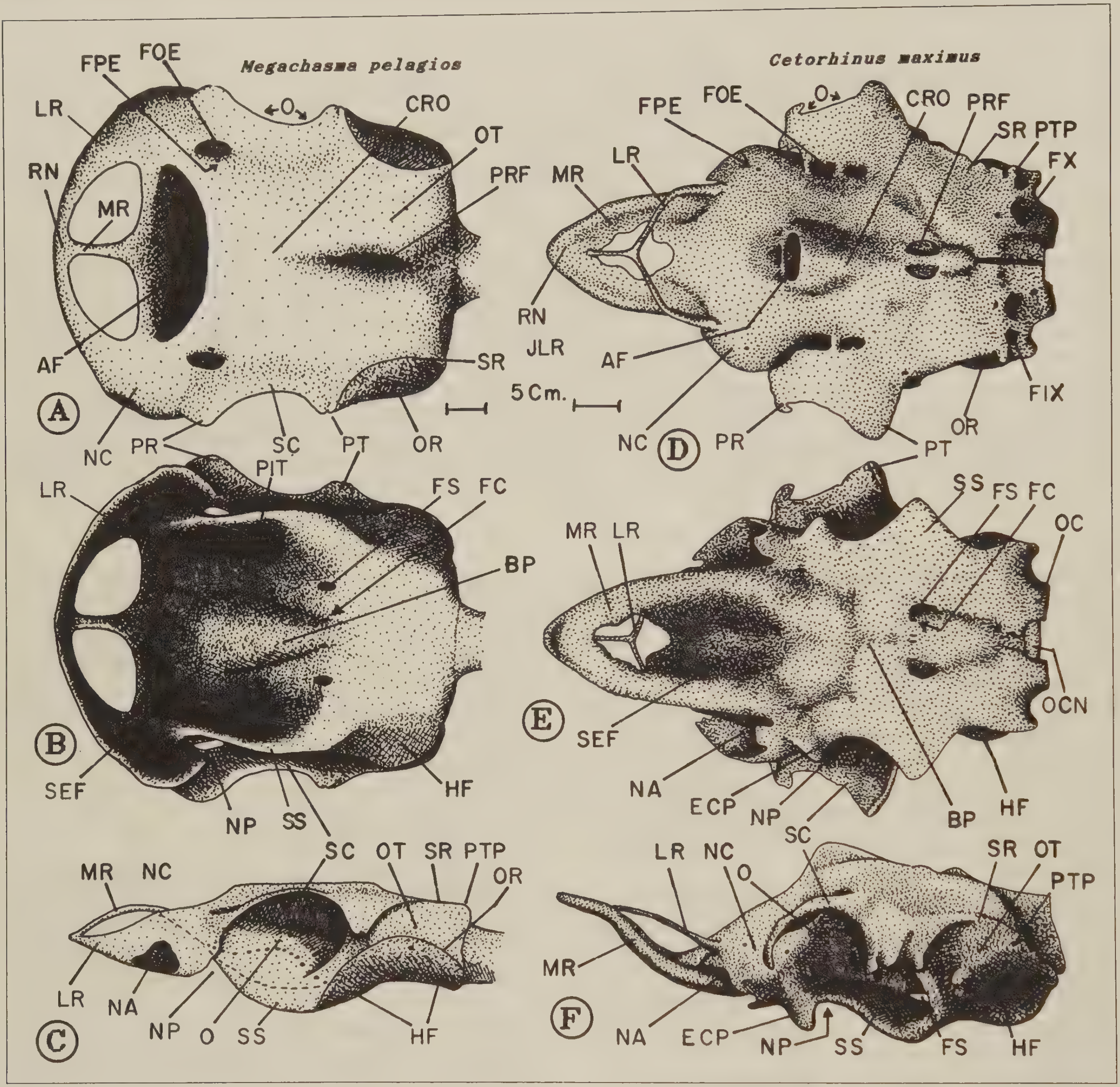
Phenetic Separation of *Megachasma* and *Cetorhinus*

Maisey's (1985) statement that the megamouth and basking sharks are confamilial is questionable on phenetic arguments. As noted by Taylor et al. (1983), the two genera are vastly divergent in morphology as befits extremely derived specialists with radically different approaches to filter feeding. Even if Maisey (1985) was correct in assuming that *Megachasma* and *Cetorhinus* were sister groups, their morphological distance merits familial separation. Characters separating these genera are summarized as follows.

Characters of *Megachasma*

TRUNK cylindrical but not highly fusiform, tapering rearward from the enormous head (Fig. 1A). Skin soft, muscles very flabby, fins soft and flexible. *Caudal peduncle* slightly compressed and without keels. Upper *precaudal pit* present but lower pit absent, upper shallow and longitudinally oval.

HEAD broad, blunt, very large and long, length greater than abdomen between pectoral and pelvic bases. *Snout* very short, depressed, and broadly rounded. *Nostrils* opposite first fourth of mouth when jaws are retracted. *Mouth* terminal on head and greatly enlarged. Upper jaw and palate iridescent, and lower jaw and tongue covered with black skin that is possibly luminescent. *Jaws* highly protrusible anteroventrally, capable of extending well forward of the snout tip. *Tongue* very large, thick and broad. *Gill openings* moderately large, not extending onto dorsal or ventral surfaces of head. Internal gill openings short, strongly screened by numerous papillose *gill rakers*, which are slender dermal papillae with cartilage cores and covered by normal imbricated denticles. The papillose gill rakers are irregularly situated in tight clusters around the gill openings and are almost certainly not shed.


Megachasma pelagios
Cetorhinus maximus
FPE
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FPE
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PIT
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SEF
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ECP
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NA
ECP
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Figure 4.

Chondrocrania of A–C, *Megachasma pelagios*, BPBM-22730, 4460 mm adult male; and D–F, *Cetorhinus maximus*, LACM-35593-1, 7010 mm adult male; in dorsal (A, D), ventral (B, E), and lateral (C, F) views. ABBREVIATIONS: AF = anterior fontanelle; BP = basal plate; CRO = cranial roof; ECP = ectethmoid process; FC = foramen for internal carotid artery; FOE = external fenestra of the preorbital canal; FPE = external profundus foramen; FS = stapedial fenestra; FIX = glossopharyngeal nerve foramen; FX = vagus nerve foramen; HF = hyomandibular facet; LR = lateral rostral cartilage; MR = medial rostral cartilage; NA = nasal aperture; NC = nasal capsule; NP = orbital notch; O = orbit; OC = occipital condyle; OCN = occipital centrum; OR = opisthotic ridge; OT = otic capsule; PR = preorbital process; PRF = parietal fossa; PIT = depression for oribital processes of palatoquadrates; PT = postorbital process; PTP = pterotic process (barely developed in *Megachasma*); RN = rostral node; SC = supraorbital crest; SEF = subethmoid fossa; SR = sphenopterotic ridge; SS = suborbital shelf.

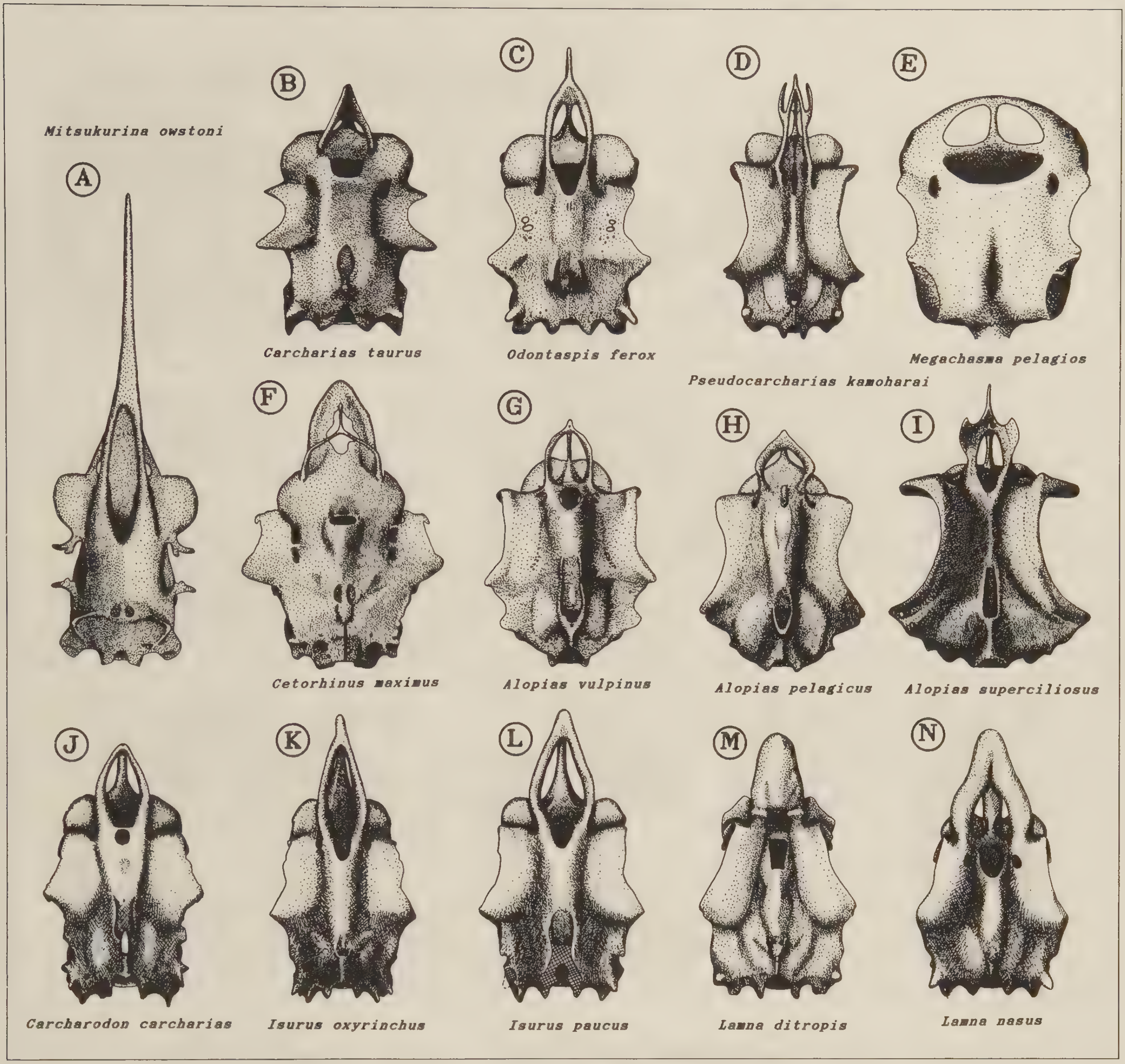
Mitsukurina owstoni
A
B
Carcharias taurus
C
Odontaspis ferox
D
Pseudocarcharias kamoharai
E
Megachasma pelagios
F
Cetorhinus maximus
G
Alopias vulpinus
H
Alopias pelagicus
I
Alopias superciliosus
J
Carcharodon carcharias
K
Isurus oxyrinchus
L
Isurus paucus
M
Lamna ditropis
N
Lamna nasus

Figure 5.

Chondrocrania of living lamnoids, in dorsal view. A, *Mitsukurina owstoni*, SU-13888, 1130 mm immature female. B, *Carcharias taurus*, CAS 1961-IX:21, 1540 mm immature female. C, *Odontaspis ferox*, LJVC-0272, 2740 mm adult male. D, *Pseudocarcharias kamoharai*, LACM-uncat., 732 mm PCL immature female. E, *Megachasma pelagios*, BPBM-22730, 4460 mm adult male. F, *Cetorhinus maximus*, LACM-35593-1, 7010 mm adult male. G, *Alopias vulpinus*, LJVC-0234, 2057 mm immature female. H, *Alopias pelagicus*, LJVC-0414, 1940 mm immature male. I, *Alopias superciliosus*, LJVC-0355, 2872 mm immature male. J, *Carcharodon carcharias*, LJVC-0187, 2045 mm immature female. K, *Isurus oxyrinchus*, LJVC-0216, 1360 mm immature female. L, *Isurus paucus*, S.P. Applegate uncat., 2175 mm adult male. M, *Lamna ditropis*, LJVC-0112, 2280 mm adult male. N, *Lamna nasus*, LJVC-880127, ~2m.

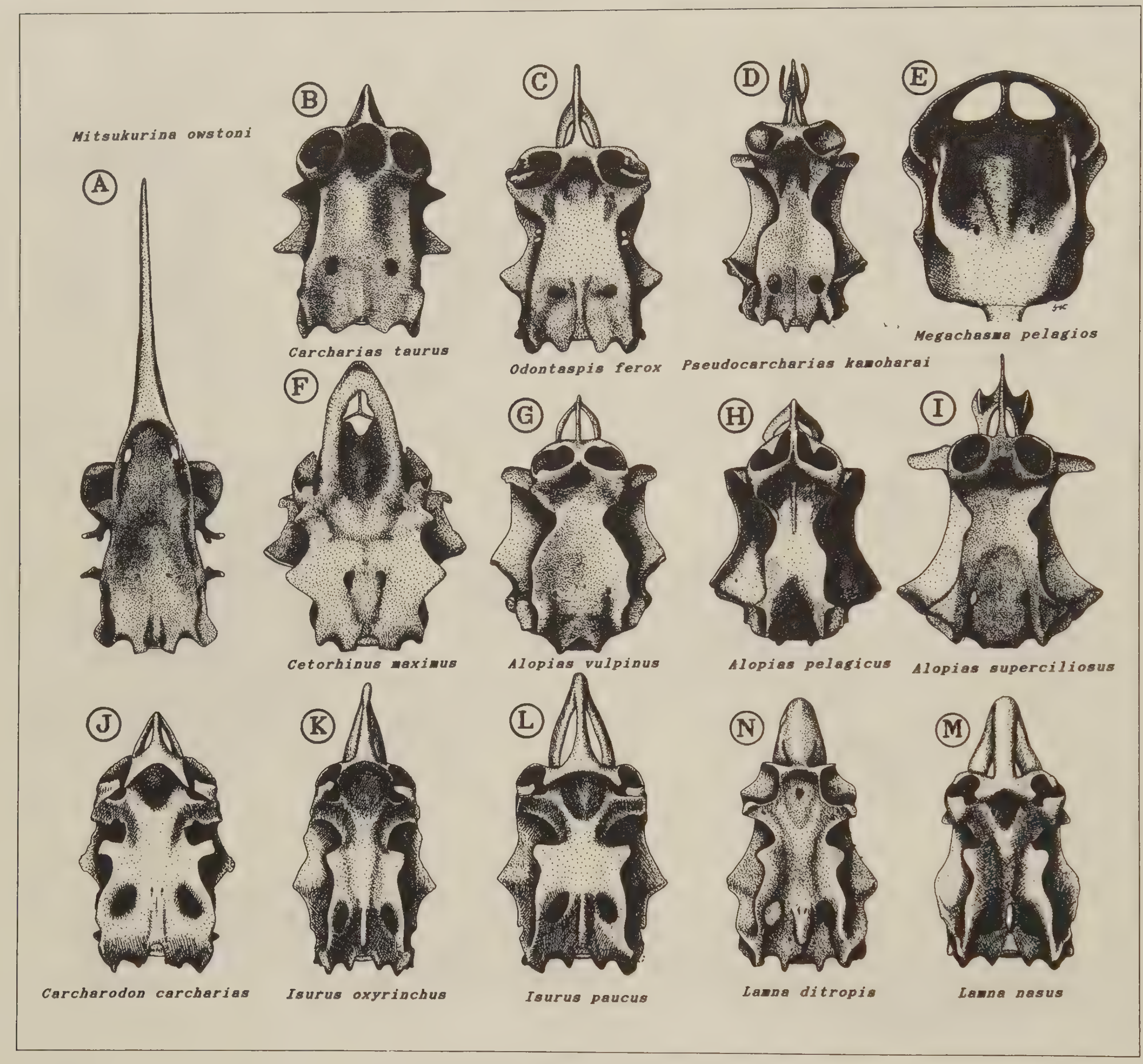
Mitsukurina owstoni
A
B
Carcharias taurus
C
Odontaspis ferox
D
Pseudocarcharias kamoharai
E
Megachasma pelagios
F
Cetorhinus maximus
G
Alopias vulpinus
H
Alopias pelagicus
I
Alopias superciliosus
J
Carcharodon carcharias
K
Isurus oxyrinchus
L
Isurus paucus
N
Lamna ditropis
M
Lamna nasus

Figure 6.
Chondrocrania of living lamnoids, in ventral view. Same specimens and lettering as Figure 5.

TEETH (Fig. 2A–D) small but about 8 mm. high in adults. Teeth not differentiated into row groups, continually varying, without a gap or small intermediate teeth between anterior and lateral teeth of upper jaw. 108/124 *rows* of teeth present. Very broad medial *toothless spaces* separating dental bands of upper and lower jaws at symphyses, broader on lower jaw than upper. Tooth *roots* moderately long, broad, and flat, with very short labial root lobes, greatly enlarged, expanded lingual protuberances, and obsolete transverse grooves. Tooth *crowns* high, narrow, recurved, flexed, and acutely tipped.

LATERAL TRUNK DENTICLES with broad, teardrop or wedge-shaped, flattened unicuspidate crowns, medial cusps not erect and directed posteriorly. Denticle *pedicles* low and broad. *Denticles* very small and flat, giving skin smooth texture. *Wavy grooves* of naked skin present on the pectoral, pelvic and caudal fin webs.

PECTORAL FINS narrowly leaf-shaped and broad-tipped, length from origin to free rear tip about half anterior margin length. *Pectoral origins* under fourth gill openings. *Pectoral area* about three times first dorsal fin area, anterior margin about 3.2 times pelvic anterior margins.

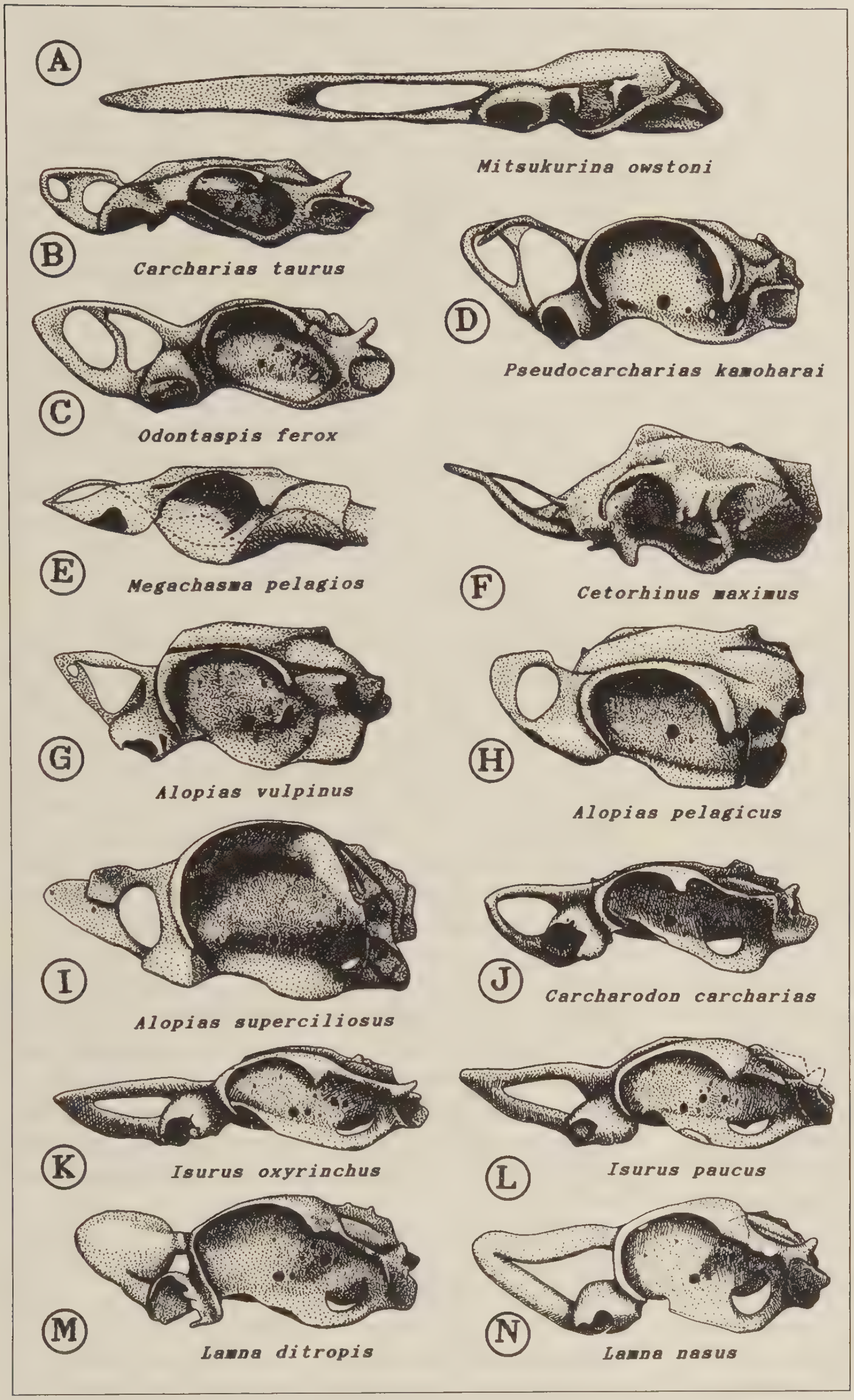
A
Mitsukurina owstoni
B
Carcharias taurus
D
Pseudocarcharias kamoharai
C
Odontaspis ferox
E
Megachasma pelagios
F
Cetorhinus maximus
G
Alopias vulpinus
H
Alopias pelagicus
I
Alopias superciliosus
J
Carcharodon carcharias
K
Isurus oxyrinchus
L
Isurus paucus
M
Lamna ditropis
N
Lamna nasus

Figure 7.
Chondrocrania of living lamnoids, in lateral view. Same specimens and lettering as Figure 5.

CLASPERS slender and cylindrical, with tapering tips, short glans and small, sharp external spurs.

FIRST DORSAL FIN low, moderately large, with a narrowly rounded apex well in front of fin insertion; first dorsal origin about opposite or slightly behind pectoral insertions, midbase much closer to pectoral fin bases than pelvic bases. First dorsal skeleton low, aplesodic. *Second dorsal fin* low and broad, about twice as large as anal fin. *Anal fin* origin about opposite free rear tip of second dorsal.

CAUDAL FIN not lunate or crescentic, very flexible and elongated, with a long upper lobe about half precaudal length of shark and a third of total length; preventral margin 43% of dorsal margin, subterminal notch weak, and no ripples or undulations present on the caudal margins; caudal vertebral axis at about 20° to body axis.

LAMNOID INTESTINAL VALVE COUNTS

	15					20					25					30					35					40					45					50					55
Mitsukurina owstoni					1																																				
Carcharias taurus														1		2																									
Odontaspis ferox																		1																							
Odontaspis noronhai																1?																									
Pseudocarcharias kamoharai										1	1	2	1																												
Megachasma pelagios										1																															
Cetorhinus maximus																																	x	x	x	x					
Alopias pelagicus																							1	-	1	1															
Alopias superciliosus																															1										
Alopias vulpinus																			1	1																					
Carcharodon carcharias																																	1	1	1	1	3	2		1	
Isurus oxyrinchus																																	2		1						
Isurus paucus																																								1	
Lamna ditropis																								1																	
Lamna nasus																									1																

Figure 8.
Intestinal valve counts of living lamnoids. Numbers of specimens counted are indicated, except in *Cetorhinus maximus* for which only a range was available (Matthews and Parker 1950). Count for *Odontaspis noronhai* after Branstetter and McEachran (1986).

CHONDROCRANIUM (Figs. 4A–C, 5E, 6E, 7E) very low and flat, extreme width across preorbital processes about equal to nasobasal length; height of cranium about 40% of nasobasal length. *Rostrum* of simple tripodal form, including a small, moderately elongated, slightly compressed medial rostral cartilage originating from the middle of the internasal plate and a pair of broad-based, triangular lateral rostral cartilages that connect anteriorly in a simple rostral node. *Medial rostral cartilage* a simple rod, without a ventral fossa. Base of medial rostral cartilage elevated by dorsally arched internasal septum above level of bases of lateral rostral cartilages and with shaft of cartilage arching anteroventrally to meet rostral node. Bases of *lateral rostral cartilages* broadly expanded and covering the entire anterior surfaces of the nasal capsules. *Rostral node* of cranium short, narrow, and depressed, without an anteroventral flange. Rostrum short, length from base of medial rostral cartilage to tip of rostral node about 26% nasobasal length, but width across outer bases of lateral rostral cartilages 2.2 times length of rostrum.

NASAL CAPSULES highly compressed, platelike, and wedge- shaped, situated mostly lateral to suborbital shelves; orbitonasal foramina medial to capsules proper. *Nasal apertures* on lateral surfaces of nasal capsules. *Subethmoid fossa* extremely broad and long, expanded anteriorly to below rostral node, between nasal capsules, and posteriorlaterally to merge with orbital pits in basal plate, molded to fit around palatine processes of palatoquadrates when jaws are retracted. External *profundus nerve foramina* well posteriormedial to nasal capsules, opposite midlengths of fenestrae for preorbital canals.

CRANIAL ROOF very broad and flat, not arched above orbits. *Anterior fontanelle* huge, transversely expanded, slightly elevated above level of nasal capsules but with dorsal edge about opposite dorsal edge of orbits. Fontanelle not housed in a separate turret above the cranial roof proper. Width of fontanelle about three times greater than its height and about 53% of nasobasal length. No pit and ridge below lower edge of fontanelle. *Parietal fossa* a single deep elongated slit, with endolymphatic and perilymphatic foramina not immediately visible.

BASAL PLATE very broad, width across orbital notches about 69% of nasobasal length, broadly arched over rear ends of palatine processes of palatoquadrates. Basal plate with a high midventral hump between interorbital septum and internal carotid foramina, but flat between carotid foramina and occiput. A pair of deep, prominent, unique *orbital pits* in the anterior third of basal plate for the orbital processes of palatoquadrates, behind the orbital notches, anterior to the stapedial and carotid openings, and just mesial to the bases of the suborbital shelves. Distance between fenestrae for *stapedial arteries* about 25% of nasobasal length. *Internal carotid foramina* well medial to stapedial fenestrae.

ORBITS nearly circular in lateral view, not expanded behind postorbital processes. *Preorbital processes* low and not much exserted from supraorbital crests. *Supraorbital crests* shallowly concave in lateral and dorsoventral view, tapering posteromesially between preorbital and postorbital processes. *Postorbital processes* short, slightly exserted from supraorbital crests, distance across them much less than distance across preorbital processes. External fenestrae for *preorbital canals* small, behind preorbital processes, and not separating their bases from the nasal capsules. *Suborbital shelves* slightly convex in ventral view, with edges nearly parallel, anterior to stapedial fenestrae, but gently tapering mesially to otic capsules behind them; *orbital notches* extremely shallow, connecting directly to bases of nasal capsules and without ectethmoid processes anterior to them or expanded lateral wings of suborbital shelves behind them. *Postorbital walls* slanting anteroventrally from below postorbital processes in lateral view.

OTIC CAPSULES with sphenopterotic ridges exserted posterodorsally from the otic capsule, ending in a blunt corner, not expanded as discrete, horn-like pterotic processes. *Opisthotic processes* greatly expanded lateral to sphenopterotic ridges, broadly arched and not undulated. *Hyomandibular facets* broadly crescentic and enormously expanded, covering entire ventrolateral faces of otic capsules and extending in front of postorbital processes onto posterior thirds of suborbital shelves. Hyomandibular facets hardly exserted rearwards from the occiput, rear ends bluntly rounded.

OCCIPUT vertical, vagus and glossopharyngeal foramina small and hardly visible in dorsal view. *Nuchal crest* hardly developed above *foramen magnum*; no medial prominence behind parietal fossa. *Occipital condyles* weak, *Occipital centrum* apparently absent and secondarily lost.

JAWS very long, thick, and stout. *Palatoquadrates* (Fig. 3D) about 1.8 times length of cranium; when retracted palatoquadrates fall with their anterior tips opposite rostral tip and extend from the rostrum to about half their lengths behind the occiput. Palatoquadrates with long, massive, straight *palatine processes* without dental bullae or mesial processes, but with strong, low, and knob-like cartilaginous *orbital processes* that fit in the orbital pits on the underside of the basal plate when the jaws are retracted. Palatoquadrates with low but strong *quadrate processes* which are hardly elevated above palatine processes; quadrate grooves hardly developed on the quadrate processes. Anterior ends of *Meckel's cartilages* ending below anterior ends of palatoquadrates, no "overbite" of latter on Meckel's cartilages. Rear ends of Meckel's cartilages extending well behind joint with palatoquadrates.

VERTEBRAL CENTRA poorly calcified, strong primary calcification of the *double cones* virtually absent and branched secondary *radii* vestigial in the intermedialia, annuli not apparent in vestigial radii; *notochordal sheath* very wide between vertebral centra.

RING INTESTINAL VALVE with 24 turns.

Characters of *Cetorhinus*

TRUNK cylindrical and fusiform, tapering anteriorly from the pectoral fins and posteriorly from the pelvics (Fig. 1B). Skin and muscles firm, fins stiff. *Caudal peduncle* depressed and with strong lateral keels. Both upper and lower *precaudal pits* present, these deep, transverse, and crescentic.

HEAD narrow, conical, pointed, and relatively short, length less than abdomen between pectoral and pelvic bases. *Snout* long, hooked and pointed in young but bluntly conical and bulbous in adults. *Nostrils* well in front of mouth. *Mouth* subterminal on head and moderately enlarged, mouth lining and tongue not iridescent or luminescent. JAWS hardly protrusible anteroventrally, but capable of distending lateroventrally. *Tongue* small and flat. *Gill openings* enormously enlarged, expanded onto dorsal and ventral surfaces of head. Internal gill openings very long, with pretrematic and posttrematic rows of unique *gill raker denticles*. These specialized denticles have compressed bases and hairlike slender crowns that do not greatly impede water flow through the gills but catch small crustaceans on mucous secreted by the pharynx; gill raker denticles are periodically shed.

TEETH (Fig. 2M–O) very small, height less than 6 mm. in adults. Teeth weakly differentiated into row groups, with a gap between anterior and lateral teeth of upper jaw. Over 200 *rows* of teeth present in upper and lower jaws of adults (one counted had 203/229 rows). Narrow *toothless spaces* separating dental bands of upper and lower jaws at symphyses. Tooth *roots* short, narrow, high, and flat, with moderately long labial root lobes, small lingual protuberances, and strong basal grooves. Tooth *crowns* short, thick, not recurved, wedge-shaped, and bluntly pointed.

LATERAL TRUNK DENTICLES with narrow, recurved, unicuspidate, erect crowns with sharp hooked cusps, directed anteriorly and dorsoventrally as well as posteriorly. *Denticles* large, skin with very rough, abrasive texture. No *wavy grooves* of naked skin present on the fin webs, but transverse and longitudinal grooves present on body.

PECTORAL FINS broad, wedge-shaped, and blunt-tipped, length from origin to free rear tip less than half anterior margin length in adults. *Pectoral origins* behind fifth gill openings. *Pectoral area* about equal to first dorsal fin area, anterior margin about twice pelvic anterior margins.

CLASPERS thick and tapering, with a long glans and heavy, blunt external spurs.

FIRST DORSAL FIN high, large, with broadly rounded apex just in front of fin insertion; first dorsal origin behind pectoral free rear tips, midbase about equidistant between pectoral and pelvic bases. First dorsal fin with high semiplesodic fin skeleton. *Second dorsal fin* high and relatively narrow, about as large as anal fin. *Anal fin* origin varying from about opposite second dorsal insertion to opposite second dorsal midbase.

CAUDAL FIN crescentic, stiff and short, with upper lobe about a fourth of precaudal length of shark, preventral margin about 2/3 of dorsal margin in adults, ripples or undulations present on the dorsal caudal margin; caudal vertebral axis at 40 to 45° to body axis in adults.

CHONDROCRANIUM (Figs. 4D–F, 5F, 6F, 7F) very high and arched between orbits but with orbits and otic capsules moderately low, extreme height of cranium about 60% of nasobasal length. *Rostrum* of greatly modified tripodal form: It includes a broad-based, hooked, elongated, greatly depressed medial rostral cartilage originating from the entire width of the internasal plate; and a pair of slender, narrow-based, cylindrical lateral rostral cartilages that connect together in a posterior false rostral node and extend as a slender medial bar anteriorly to the rear of the true rostral node. *Medial rostral cartilage* complex, formed as a pair of thick lateral bars separated by a thin mesial plate that forms the anterior extension of the subethmoid fossa on the underside of the cartilage, but thickening anteriorly to form the rostral node. Base of medial rostral cartilage not elevated above bases of lateral rostral cartilages and with cartilage arching anterodorsally to meet rostral node. Bases of *lateral rostral cartilages* very narrow, attached to anterodorsomesial edges of nasal capsules and not covering their entire surfaces. *Rostral node* of cranium long, broad, and greatly depressed, with a ventral fossa at its tip. Rostrum long, length from base of medial rostral cartilage to tip of rostral node about 50% of nasobasal length in adult, width across outer bases of lateral rostral cartilages 1.2 in length of rostrum.

NASAL CAPSULES subspherical, situated anterior to suborbital shelves, orbitonasal formaina medial to capsules proper. *Nasal apertures* on ventral surfaces of nasal capsules. *Subethmoid fossa* deep but relatively narrow and long, expanded anteriorly between nasal capsules to below base of medial rostral cartilage but not molded around palatine processes of palatoquadrates. External *produndus nerve foramina* on dorsal midlengths of nasal capsules, well in front of external fenestrae for preorbital canals.

CRANIAL ROOF moderately broad and humped, arched far above orbits. *Anterior fontanelle* small, subcircular, not transversely expanded, far above levels of nasal capsules and orbits; fontanelle housed in a scooplike turret rising above the cranial roof proper. Width of fontanelle about 1.3 times its height and about 14% of nasobasal length. A prominent pit and ridge present below lower edge of fontanelle. *Parietal fossa* formed as a pair of shallow oval depressions separated by a broad ridge, with endolymphatic and perilymphatic formaina visible.

BASAL PLATE very broad, width across orbital notches about 57% of nasobasal length, not arched over palatine processes of palatoquadrates. Basal plate virtually flat between interorbital septum and internal carotid foramina, and from carotid foramina and occiput, but with a slight basal angle at carotids. No *orbital pits* in the anterior third of basal plate for the orbital processes of palatoquadrates. Distance between *stapedial fenestrae* about 11% of nasobasal length. Foramina for *internal carotid arteries* on anteromedial edges of stapedial fenestrae.

ORBITS elongated in lateral view, extending about half their lengths behind front edges of preorbital processes and divided into anterior and posterior lobes by them. *Preorbital processes* high, recurved, and exserted from supraorbital crests. *Supraorbital crests* deeply concave in lateral and dorsoventral view, expanding posterolaterally between preorbital and postorbital processes. *Postorbital processes* long, strongly exserted from supraorbital crests, distance across them greater than distance across preorbital processes. External fenestrae for *preorbital canals* enlarged, multiple, expanded anteriorly and posteriorly to perforate bases of preorbital processes and front of supraorbital crests. *Suborbital shelves* undulated in ventral view, with anterior ends exserted as prominent *ectethmoid processes* that extend lateroventrally from nasal capsules and limit travel of palatoquadrates anterior to orbits, deep *orbital notches* extending posteroventrolaterally into acute, broad, triangular *lateral wings*, then abruptly posterodorsomedially to otic capsules. *Postorbital walls* slanting posteroventrally from below postorbital processes in lateral view.

OTIC CAPSULES with sphenopterotic ridges not exserted posterodorsally from the otic capsule, ending in short, blunt hornlike *pterotic processes*. *Opisthotic processes* slightly expanded lateral to sphenopterotic ridges, slightly undulated. *Hyomandibular facets* oval and large, covering ventrolateral faces of otic capsules but not expanded onto suborbital shelves. Hyomandibular facets exserted rearwards from the occiput, rear ends bluntly angular.

OCCIPUT canted diagonally from anterodorsal to posteroventral, vagus and glossopharyngeal foramina huge and prominently visible in dorsal view. *Nuchal crest* strongly developed above *foramen magnum*; a truncated, abruptly elevated medial projection anterior to nuchal crest and just behind parietal fossa. *Occipital condyles* high and stout, *occipital centrum* strongly developed.

JAWS relatively slender and thin. *Palatoquadrates* (Fig. 3F) slightly less than cranial length; when elevated palatoquadrates fall with their anterior tips below the midbases of the nasal capsules and extend about a third of their lengths behind the occiput. Palatoquadrates with slender posteriorly tapering *palatine processes* without dental bullae or mesial processes; *orbital processes* obsolete, reduced to low ridges connecting the ethmopalatine ligaments to the region of the ectethmoid processes and orbital notches. Palatoquadrates with moderately high *quadrate processes* which are prominently elevated above palatine processes; quadrate grooves well developed on the quadrate processes. Anterior ends of *Meckel's cartilages* ending slightly behind anterior ends of palatoquadrates, with an ''overbite'' of latter on Meckel's cartilages. Rear ends of Meckel's cartilages not expanded behind joints with palatoquadrates.

VERTEBRAL CENTRA strongly calcified, with strong primary calcification of the *double cones* well developed, and prominent branched secondary *radii* and interconnecting *annuli*. *Notochordal sheath* relatively narrow between vertebral centra.

RING INTESTINAL VALVE with 47–50 turns.

Phyletic Relationships of *Megachasma* and Other Lamnoids

Although phenetic distance supports the separation of Megachasmidae and Cetorhinidae, the question remains as to whether these families are sister groups. Maisey (1985, fig. 2) suggested five sets of synapomorphies for *Megachasma* and *Cetorhinus*: 1) Modified ethmopalatine articulation; 2) Suborbital shelf interposed between palatoquadrate and orbit; 3) Median rostral cartilage partially dorsal to lateral rostral bars; 4) Simplified tooth cusp and root morphology, loss of dental differentiation, increase in numbers of tooth rows; 5) Enlarged gill rakers extending to margins of gill openings, covered by modified oropharyngeal scales.

Maisey's first and second characters refer to supposedly derived similarities in the cranial-palatoquadrate articulation in the megamouth and basking sharks, which he implied were not shared by other lamnoids. In *Megachasma* the orbital processes fit into deep pits in the basal plate (Fig. 3D) and the suborbital shelves wrap dorsolaterally around the palatoquadrates and exclude them from orbital contact. The basking shark has a pair of shallow depressions on the basal plate near the orbitonasal foramina, from which connective tissue arises and extends as the ethmopalatine ligaments to the palatoquadrates (Fig. 3F). Maisey considered these depressions as synapomorphies in the basking and megamouth sharks. However, depressions near the orbitonasal foramina are universal on the basal plates of lamnoid chondrocrania (Fig. 6). In groups with discrete orbital processes (odontaspidids, Fig. 3B; and alopiids, Fig. 3E) or long suspensory ethmopalatine ligaments (mitsukurinids, Fig. 3A), these depressions form part of the orbital suspensory points for the palatoquadrates as in *Cetorhinus*. In *Pseudocarcharias*, with the orbital processes apparently merged with the large dental bullae on the palatoquadrates (Fig. 3C), and in the Lamnidae, with the orbital processes absent (Fig. 3G), the ethmopalatine ligaments have a more diffuse but generally similar arrangement in linking the palatoquadrates with these depressions.

The basking shark also has, as supposed equivalents of the modified suborbital shelves of the megamouth shark, a pair of ventrally expanded ectethmoid processes anterolateral to the palatoquadrates and orbital notches. However, ectethmoid processes, as separate entities from the suborbital shelves, are absent from *Megachasma* and mitsukurinids, pseudocarchariids, odontaspidids, and alopiids. Ectethmoid processes are present in Lamnidae (Fig. 3G) albeit less prominently developed than in *Cetorhinus* (Fig. 3F), and are suggested as synapomorphies of these groups. In cetorhinids and lamnids the ectethmoid processes may serve to restrict anterior travel of the palatoquadrates, and do not exclude the palatoquadrates from the orbits.

No other lamnoids have the unique, highly derived suspensory arrangement of *Megachasma*, which has no synapomorphies with *Cetorhinus* that are absent in other lamnoids. However, *Cetorhinus* can be allied to the Lamnidae by its jaw suspension.

Maisey's third character is absent from *Cetorhinus*, which has a ventrally situated medial rostral cartilage as in lamnoids other than *Megachasma* (Figs. 4F, 7A-N).

. Maisey's fourth character set, decreased heterodonty, is probably derived in *Cetorhinus* and *Megachasma*. However, it could be the result of parallel loss or reduction of heterodonty rather than descent from an immediate common ancestor with secondarily homodont teeth. Large teeth with disjunct heterodonty (Compagno 1970) are present in lamnoids that are not filter feeders, but reduced, numerous, weakly heterodont teeth are present in two other nonlamnoid groups of filter feeders, the orectoloboid whale shark (*Rhincodon typus*, family Rhincodontidae) and the devil rays (family Mobulidae). The false catshark (*Pseudotriakis microdon*, family Pseudotriakidae) is a carcharhinoid with gradient heterodonty and numerous small teeth but apparently is not a filter feeder.

Detailed comparison of the tooth morphology of *Megachasma* and *Cetorhinus* reveals important differences. *Megachasma* has teeth with large functional crowns and needle-sharp cusps (Fig. 2A-C) similar to those of more primitive nonfiltering lamnoids (Odontaspididae, Mitsukurina, Pseudocarcharias). In contrast, the crowns of *Cetorhinus* teeth are very reduced, blunt-tipped, and wedge-shaped (Fig. 2M-O), and resemble *Rhincodon* teeth (Fig. 2P, R). The roots of *Megachasma* teeth are derived in their reduced labial lobes, enlarged lingual protuberance, horizontal attachment surface, and possibly in the loss of a transverse groove. *Cetorhinus* teeth retain well-developed labial lobes, transverse grooves, and a small lingual protuberance.

Maisey's fifth character set combines two radically different arrangements for filter feeding. The specialized denticle gill rakers of *Cetorhinus* and supporting filtration structures are unique among Chondrichthyes, and resemble the bony gill rakers and slender gill arches in many filter feeding teleosts. The dense papillose gill rakers of *Megachasma* are like sparser papillose gill rakers in nonfiltering squalomorph sharks and some carcharhinoids (Compagno 1988). The gill rakers of *Megachasma* also resemble the more specialized filter screens of *Rhincodon* and the filter plates of mobulids in being cartilage-cored and covered by skin and normal denticles.

It is unlikely that the divergent filtration setups in *Megachasma* and *Cetorhinus* could be derived from each other or from a common filtering ancestor, but each of the setups could be separately derived from two different types of nonfiltering precursors. That of *Megachasma* is derivable from the more primitive arrangement seen in the Odontaspididae, while that of *Cetorhinus* is derivable from the arrangement found in the Lamnidae. Hence filter feeding cannot be considered a synapomorphic character of *Cetorhinus* and *Megachasma*. The divergent functional implications of the megachasmid and cetorhinid feeding apparatuses are discussed below.

The ranking of the megamouth and basking sharks as immediate sister groups is not supported by the evidence cited above. The following cladistic analysis of the order Lamniformes attempts to relate the megamouth shark to other living lamnoids. The analysis is a first approximation that uses the simple Hennigian noncomputer method of clustering derived taxa, the schema of cladistic argument, and the rationale for determination of character polarities of Compagno (1988). Questionable polarities are labeled with a query (?). The branches of the lamnoid cladogram (Fig. 9) are numbered according to the text arguments below.

1. Synapomorphies of the order Lamniformes: Lamnoid tooth pattern; reduction of labial cartilages; elongated ring intestinal valve with over 15 turns; uterine cannibalism(?); development of primarily exochordal radii in vertebral centra.

2a. Autapomorphies of *Mitsukurina owstoni* (Mitsukurinidae). Skin thin and soft, fins very flexible, muscles flabby; snout greatly elongated and paddle-shaped; mouth elongated, expanded anteriorly to just behind nostrils; gill region and throat between lower jaws naked, skin there very thin, pliable, and elastic, forming a pelican-like pouch between the Meckel's cartilages and the basihyals and ceratohyals; intermediate teeth lost; anterolateral teeth with extremely slender, needle-like cusps and very thin, flat, expanded labial root lobes; lateral trunk denticles with narrow, conical, hooked, unicuspidate, semi-erect crowns; pectoral fins smaller than pelvic and anal fins; dorsal fins very small and rounded, not angular; anal fin low and elongated, much larger than dorsal fins; insertion of anal fin separated by notch from ventral caudal lobe; caudal fin elongated, dorsal caudal lobe hardly elevated(?), ventral caudal lobe not expanded(?); rostrum greatly elongated, about 1.5 times nasobasal length; tripodal rostrum highly modified, medial rostral cartilage basally expanded to the width of the internasal plate but tapering to a narrow rod distally before joining the rostral node; lateral rostral cartilages connecting anteriorly in a short, common, flattened triangular plate that joins with the rostral node; rostral node a long, greatly compressed, distally angular plate; subethmoid fossa expanded anteriorly into base of medial rostral cartilage but not displacing that cartilage dorsally, fitting anterior ends of palatine processes of palatoquadrates; supraorbital crests absent, preorbital and postorbital processes distally trilobate or bilobate; opisthotic ridges greatly expanded laterally; palatoquadrates with distally bent palatine processes; orbital processes reduced to low ridges on the palatine processes, processes continuous with attenuated, elastic ethmopalatine ligaments that attach to the nasal capsules; mandibular joint of Meckel's cartilages greatly expanded dorsally in a fanlike articular hinge; rear ends of Meckel's cartilages extending well behind joint with palatoquadrates; vertebral calcification reduced, radii simple.

2b. Synapomorphies of all other lamnoids. Transverse ridges lost on tooth cusps in anterolateral teeth, reduced ridges sometimes present on basal ledges; precaudal pits developed; development of enlarged stapedial fenestrae on cranium that house highly convoluted basal arteries. (3).

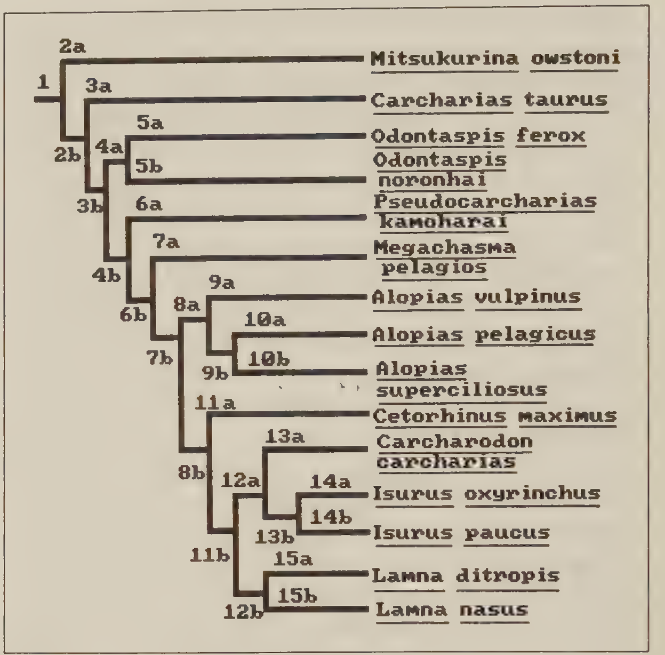

Figure 9.
Cladogram of lamnoid interrelationships. For explanation see text.

3a. Autopomorphies of *Carcharias taurus* (Odontaspididae in part). Posterior shift of first dorsal fin(?); air-gulping buoyancy mechanism; arching of basal plate below anterior part of suborbital shelves(?).

3b. Synapomorphies of all other lamnoids (except taxa above). First dorsal fin much larger than second; no first upper anterior tooth, this replaced by upper symphysical or lost. (4).

4a. Autapomorphies of *Odontaspis* (Odontaspididae in part). Bulbous snout(?); teeth reduced in size; elongated trunk relative to head and precaudal tail; enlarged vertical fenestra in rostrum(?) (5).

4b. Synapomorphy of other lamnoids (*Pseudocarcharias* and "advanced" lamnoids). Reduction of third lower anterior teeth to size and shape of lateral. (6).

5a. Autapomorphies of *Odontaspis ferox*. Intermediate teeth increasing to three to five rows(?); anterolateral teeth usually with two or three pairs of cusplets.

5b. Autapomorphies of *Odontaspis noronhai*. Labial lobes of anterolateral teeth expanded; anal fin reduced; color uniform dark brown.

6a. Autapomorphies of *Pseudocarcharias kamoharai* (Pseudocarchariidae). Low keels on sides of caudal peduncle; trunk elongated relative to head and tail; underside of snout between nostrils and mouth with a distinct angular ventral projection, noticeable when jaws are fully retracted; eyes enlarged; labial furrows lost; gill openings moderately enlarged; no symphysial teeth, number of rows of posterior teeth reduced, less than 30 rows of teeth in each jaw; anal fin base narrow, semipivotable; cranium elevated;

rostral node with slender rostral appendices and enlarged vertical fenestra; nasal capsules depressed below level of basal plate, only narrowly separated by internasal septum; internasal septum with a unique wedge-shaped ventral process; subethmoid fossa very narrow; cranial roof very narrow and acutely arched; anterior fontanelle a narrow vertical slot; basal plate and suborbital shelves very narrow; orbits extremely large; postorbital processes extending ventrally to form loose articulations with quadrate processes of palatoquadrates; otic capsule shortened; palatine processes shortened on palatoquadrates; orbital processes merged into high, dorsally expanded dental bullae that articulate with the orbital notches of the cranium rather than the posteroventral surfaces of the nasal capsules; quadrate processes with an angular articular surface that contacts the postorbital processes; vertebral radii slightly reduced; adults to 1.1 m long.

6b. Synapomorphy of "advanced" lamnoids (Megachasmidae, Alopiidae, Cetorhinidae, Lamnidae). Plesodic pectoral fins. (7).

7a. Autapomorphies of *Megachasma pelagios* (Megachasmidae). Skin soft, muscles very flabby, fins soft and flexible (paralleled by *Mitsukurina owstoni*); upper precaudal pit fossate; head enlarged; snout very short, blunt and broadly rounded; nostrils opposite mouth; mouth terminal; mouth with iridescent and possibly luminescent tissue; tongue and pharynx greatly enlarged; numerous cartilage-cored gill raker papillae present; teeth reduced in size but increased in number, over 100 rows in each jaw; medial toothless spaces enlarged; disjunct monognathic heterodonty lost; labial root lobes reduced, lingual protuberances expanded on tooth roots; wavy grooves of skin on fins; pectoral fins of straight, elongated, terminally expanded "oceanic" type; pectoral origins under fourth gill openings; caudal fins elongated, subterminal notch weak, no lateral undulations on dorsal caudal margin; chondrocranium depressed and extremely broad; rostrum extremely short; rostral node simple; medial rostral cartilage elevated above lateral rostrals; bases of lateral rostral cartilages covering nasal capsules; nasal capsules compressed and wedge-shaped, lateral to suborbital shelves; nasal apertures entirely lateral; subethmoid fossa greatly expanded; cranial roof very broad and flat; anterior fontanelle greatly expanded laterally; parietal fossa a single deep slit; basal plate with high midventral hump and deep orbital pits; postorbital walls slanting anteroventrally; opisthotic processes greatly expanded lateral to sphenopterotic ridges; hyomandibular facets expanded onto suborbital shelves; occiput vertical; occipital condyles weak and occipital centrum lost; jaws greatly enlarged, palatoquadrates nearly twice length of cranium and extending to rostral tip when retracted, capable of being protruded far anterior to rostrum; orbital processes articulating with the cranial basal plate and not the orbital notches; palatine processes without dental bullae; palatoquadrates fitting between suborbital shelves, nasal capsules and lateral rostral cartilages when retracted and excluded from orbital contact; quadrate processes low on palatoquadrates, quadrate grooves hardly developed; Meckel's cartilages expanded anteriorly to opposite palatoquadrates, no "overbite"; rear ends of Meckel's cartilages extending well behind joint with palatoquadrates (Taylor et al. 1983, fig. 14); vertebral calcification greatly reduced, radii vestigial, notochordal sheath expanded between vertebral centra.

7b. Synapomorphies of Alopiidae, Cetorhinidae, and Lamnidae. First dorsal fin elevated, fin skeleton partially expanded into fin web (semiplesodic); jaws not strongly protrusible; intestinal valve counts increasing to a range of 33–55. (8).

8a. Synapomorphies of *Alopias* (Alopiidae). Eyes enlarged; pectoral origins under third or fourth gill openings(?); pelvic fins enlarged and plesodic; second dorsal and anal fins greated reduced, with pivoting bases (paralleling the Lamnidae); upper lobe of caudal fin elongated, whiplike and about as long as body; chondrocranium very high between orbits, orbits enlarged; internasal septum high and compressed, with nasal capsules mesially adjacent; otic capsules shortened; mouth, jaws, and teeth reduced in size; vertebral counts increased to over 280 total. (9).

8b. Synapomorphies of Cetorhinidae and Lamnidae. Body spindle-shaped, caudal peduncle depressed and with strong lateral keels; labial furrows absent; gill openings enlarged; caudal fin shortened and lunate; presence of ectethmoid processes on chondrocranium that limit jaw protrusion; suborbital shelves with prominent lateral wings behind orbital notches. (11).

9a. Autapomorphies of *Alopias vulpinus*. Claspers extremely slender, clasper spurs lost(?).

9b. Synapomorphies of *Alopias pelagicus* and *A. superciliosus*. Eyes enlarged relative to *A. vulpinus*; labial furrows reduced or lost; nuchal grooves present above branchial region (inconspicuous in *A. pelagicus*); pectoral fins with broadened tips; ribs of monospondylous vertebrae modified to form an anterior haemal canal protecting the aorta, and extending nearly to cranial occiput; lateral rostral cartilages thickened and laterally expanded; vertical fenestra through rostral node lost; anterior fontanelle blocked and compressed anteriorly by large anterior myodomes for oblique eye muscles in orbits; orbits enlarged posteriorly to opposite stapedial fenestrae; intestinal valve counts increasing to a range of 37–45. (10).

10a. Autapomorphies of *Alopias pelagicus*. Pectoral fins of "oceanic" type, straight and with very broad tips; caudal tip extremely slender; teeth very small; nasal capsules diagonally expanded; basal plate and suborbital shelves very narrow; orbits ventrally depressed on cranium; area on basal plate between hyomandibular facets deeply concave; vertebral radii distally fused in intermedialia; vertebral counts increased to a range of 453–477 total, the highest of any living shark.

10b. Autapomorphies of *Alopias superciliosus*. Nuchal grooves deep, giving head a notched dorsolateral profile; eyes greatly enlarged, orbits modified for a vertical, binocular field of view; intermediates and most posterior teeth lost; first dorsal midbase closer to pelvic bases than pectorals; rostral appendices present on rostral node; rostral node expanded anteriorly as vertical plate; orbits enormously enlarged, with preorbital processes greatly expanded laterally; medial walls of orbit virtually touching each other, with cranial cavity highly compressed between them; optic pedicels reduced to low pads; vertebral calcification simplified, radii reduced in number(?); intestinal valve counts increasing to 45.

11a. Autapomorphies of *Cetorhinus maximus* (Cetorhinidae); Snout hooked in young; jaws hardly protrusible anteroventrally but distensible ventrolaterally; pharynx capable of great distension when feeding; tongue reduced in size; gill openings nearly encircling head; unique denticle gill rakers present; teeth greatly reduced in size and in over 200 rows in adults; no intermediate tooth rows in upper jaw; lateral trunk denticles hooklike and with crowns directed anteroposteriorly as well as ventrally; claspers very large and thick, clasper spurs greatly enlarged; cranium very high between orbits but orbits relatively low; rostrum of unique form, with broad, flat medial rostral cartilage hollowed anteroventrally by the subethmoid fossa, and T-shaped lateral rostral cartilages that fuse in a separate bar before reaching rostral node; bases of lateral rostral cartilages far anterior on nasal capsules; cranial roof arched far above orbits; anterior fontanelle housed in a discrete turret above the cranial roof proper; a pit and ridge below fontanelle; foramina for internal carotid arteries on anteromedial edges of stapedial fenestrae; preorbital processes and supraorbital crests partly separated from cranium by enlarged preorbital canals; postorbital processes enlarged, strongly notched; ectethmoid processes enlarged and ventrally directed; hyomandibular facets enlarged, covering ventrolateral faces of otic capsules; vagus and glossopharyngeal foramina enlarged; palatine processes of palatoquadrates very slender, without dental bullae; vertebral intermedialia with strong annuli; and possibly low vertebral numbers (total count of 110 in two individuals listed by Springer and Garrick 1964); gigantic size, 6–12 + m.

11b. Synapomorphies of Lamnidae. Second dorsal and anal fins greatly reduced in size and attenuated, bases pivoting; claspers with lateral dermal folds; rostral node without a lateral fenestra; nasal capsules depressed below level of basal plate; orbital notches deeply incised; orbits expanded posteriorly to level of pterotic processes; stapedial fenestrae greatly enlarged; mesial processes present at symphysial joints of palatoquadrates. (12).

12a. Synapomorphies of *Carcharodon* and *Isurus*. Jaws and anterior teeth enlarged; lateral cusplets lost on teeth or present only in very young(?); intestinal valves increasing to a range of 47–55; increase in total vertebral counts to a range of 170–197(?); increase in size in adults to at least 4 m maximum. (13).

12b. Synapomorphies of *Lamna*. Secondary caudal keels present; bases of lateral rostral cartilages elevated far above nasal capsules, originating on bases of preorbital processes; orbits elevated above cranial roof; cranial roof narrowed; rostral cartilages swollen and hypercalcified. (15).

13a. Autapomorphies of *Carcharodon carcharias*. Jaws and jaw muscles more enlarged than those in *Isurus*; teeth serrated and compressed, with heterodonty lessened between row groups of upper and lower jaws to produce an integrated slicing dentition; eyes and orbits reduced (?); cranium usually with a discrete epiphysial fenestra, separated from anterior fontanelle by transverse bar; cranium enlarged relative to rest of shark, strengthening jaw support; rostral cartilages reduced, rostral node relatively small; great size, 3.8–6 + m in adults.

13b. Synapomorphy of *Isurus*. Anterior teeth flexed. (14).

14a. Autapomorphies of *Isurus oxyrinchus*. Snout acutely pointed; anterior teeth more highly flexed; cranium elongated; rostrum narrowed; ethmoid region anteriorly expanded.

14b. Autapomorphy of *Isurus paucus*. Enlarged "oceanic" pectoral fins.

15a. Autapomorphies of *Lamna ditropis*. Snout shortened; upper anterior and lateral teeth with oblique cusps; hypercalcified rostral node engulfing rostral cartilages in adults.

15b. Autapomorphy of *Lamna nasus*. Free rear tip of first dorsal fin abruptly white.

The analysis indicates that the lamnoids with plesodic pectoral fins form a derived group, but that *Megachasma* has primitive characters found in aplesodic lamnoids that makes the family Megachasmidae the plesiomorphic sister group of the Alopiidae and Cetorhinidae and Lamnidae. These include its low first dorsal fin with aplesodic skeleton, low intestinal valve counts, highly protrusible jaws, and probably also the odontaspididlike size, shape, and spacing of its dorsal, anal and pelvic fins. This also supports the continued separation of the Megachasmidae and Cetorhinidae. The analysis rejects the hypothesis that the megamouth shark is the primitive sister of all other lamnoids.

The family Cetorhinidae is proposed as the sister group of the Lamnidae, while Cetorhinidae plus Lamnidae is the sister group of Alopiidae. The taxa of living Lamnidae need further study, although the ranking of *Isurus* and *Carcharodon* as sister genera and as the sister of *Lamna* seems reasonably clear. The family Alopiidae shows a very clear arrangement, with the common thresher (*Alopias vulpinus*) being the plesiomorphic sister species of the pelagic thresher (*A. pelagicus*) and bigeye thresher (*A. superciliosus*). Both Lamnidae and Alopiidae show strong evidence of being monophyletic.

There are problems with the cladogram (Fig. 9) and supporting arguments that resemble those found in carcharhinoids (Compagno 1988). As with advanced carcharhinoids the derived lamnoids with plesodic pectoral fins sort out well cladistically, but the more primitive aplesodic taxa presently do not. *Mitsukurina* is plausable as the primitive sister group of all other lamnoids, but also has numerous unique and parallel derived characters that obscure its primitiveness. Alternatively *Carcharias* and *Mitsukurina* might stand as sister groups on dentitional and cranial similarities, and likewise for *Odontaspis* and *Pseudocarcharias*. The present arrangement makes Odontaspididae paraphyletic, but this is on weak evidence and needs further study. The two *Odontaspis* species need detailed anatomical comparison to clarify their relationships to each other and to *Pseudocarcharias*. *Odontaspis noronhai* has a low anal fin and relatively large eyes as does *Pseudocarcharias kamoharai*, and may be related to it. The case for *Pseudocarcharias* as the plesiomorphic sister of the plesodic "advanced" lamnoids is weak, as its lateralized third lower anteriors may have evolved in parallel with those of the higher lamnoids. Some of these problems will be considered elsewhere and may be resolved by additional data on little-known taxa and character systems and by use of computer-aided methods of phylogenic analysis.

A problem with lamnoids that is not apparent with carcharhinoids is that most of the taxa are highly autapomorphic and have relatively few synapomomorphies with one another. Also, most taxa of lamnoids are extinct and are known mostly from fossil teeth; this lack of direct evidence makes comparison difficult and suggests that phylogenetic reconstruction based on living species is only a small fraction of the pattern of lamnoid evolution.

Megachasma and Its Possible Fossil Relatives

A comparison of the teeth of *Megachasma pelagios* as presently known (Fig. 2A–D) with fossil *Megascyliorhinus* teeth and unnamed fossil teeth from California and Oregon suggests that the fossils may be megachasmids but should be retained in separate genera. *Megascyliorhinus* teeth have far smaller, more primitive, more strongly bilobate roots and less recurved cusps (Fig. 2E–I) than those of *Megachasma*. The unnamed fossil teeth (Fig. 2J–L) have lower cusps and stronger labial root lobes than those of *Megachasma* and also have tiny cusplets. A difficulty in comparing teeth of the living *Megachasma pelagios* with megachasmidlike fossils is that the three known megamouth specimens are adult males. It is possible that some of the differences between the teeth of male *Megachasma pelagios* and megachasmidlike fossil teeth are the result of sexual heterodonty. The teeth of adult male *Megachasma* are extremely sharp and might be specially enlarged and modified for use in gripping females during courtship. Adult males of some carcharhinoid sharks have enlarged, modified, hooked cusps and lingually expanded root protuberances (Compagno 1988). However, to my knowledge fossil teeth with *Megachasma*-like elongated cusps, reduced labial root lobes and greatly expanded lingual protuberances have not been found.

Compagno (1988) mentioned material of a Cretaceous anacoracid shark, *Squalicorax "falcatus"* (possibly = *S. pristodontus*) in the LACM paleontological collections, including a largely intact chondrocranium with associated teeth and jaw fragments (LACM-VP-16056), and material of the vertebrae, teeth, and even a whole-bodied specimen which shows a high precaudal vertebral count and plesodic pectoral fins. G. Hubbell (JAWS International, Miami, Florida, pers. commun., 1988) kindly provided photographs of two other *Squalicorax* specimens in private collections for comparison with the LACM material, including an intact head and a nearly complete skeleton missing gill arches and some fin elements.

The *Squalicorax* chondrocranium (reconstruction, Fig. 10) is suggestively like that of *Megachasma* in its extreme width and general shape, except for the ethmoid region, which is highly truncated in the *Squalicorax* cranium examined and may be missing most of the rostrum (as suggested by other *Squalicorax* specimens). The characteristic modifications of the ethmoid region and basal plate of *Megachasma*, which allow the cranium to sit atop the palatine processes of the palatoquadrates, are absent in *Squalicorax*. The palatoquadrated are too fragmentary in the material examined to determine the exact nature of the orbital articulations of the palatoquadrate in *Squalicorax*, but there is no indication of a specialized megachasmid arrangement. The cranium of LACM-VP-16056 is highly calcified but crushed flat, and peripherally damaged so that details of the nasal capsules, rostrum, and orbits are uncertain. The strongly calcified jaws and vertebrae, stiff plesodic pectoral fins, caudal fin with strong ventral lobe, and large, serrated cutting teeth of *Squalicorax* suggest that it was an active, formidable macropredator rather than a sluggish filter feeder. The cranial similarities of *Megachasma* and *Squalicorax* may be superficial only, and may not be indicative of relationship, but this is uncertain with the present material.

A Revised Scenario for Megamouth Feeding

Taylor et al. (1983) compared the filter feeding apparatuses of the megamouth, basking, and whale sharks and noted important differences between them. They suggested that "*Megachasma* can be imagined as slowly swimming through schools of euphausiid shrimp and possibly other prey with jaws widely opened, occasionally closing its mouth and contracting its pharynx to expel water and

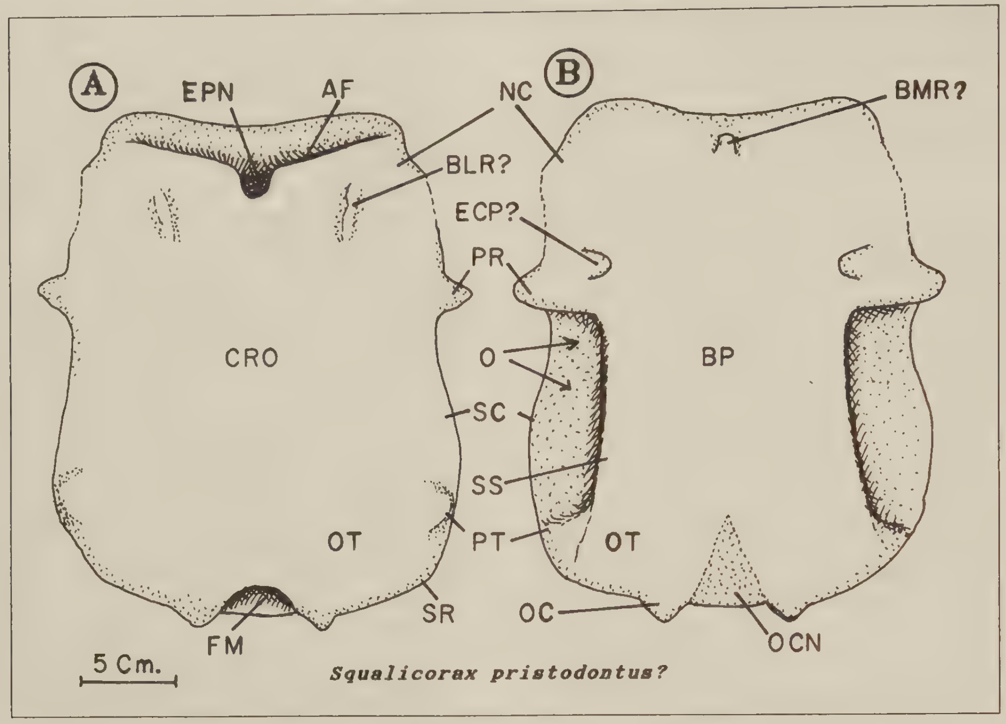

Figure 10.
Reconstruction of partial chondrocranium of *Squalicorax* "*falcatus*" (? = *S. pristodontus* [Agassiz, 1843]) in A, dorsal; and B, ventral views, based on LACM-VP-16056 (Upper Cretacous, Logan Co., Kansas). ABBREVIATIONS: AF = anterior fontanelle; BLR? = possible base of lateral rostral cartilage; BMR = possible base of medial rostral cartilage; BP = basal plate; CRO = cranial roof; ECP? = possible ectethmoid process; EPN = epiphysial notch for pineal organ; FM = foramen magnum; NC = nasal capsule; O = orbit; OC = occipital condyle; OCN = occipital centrum; OT = otic capsule; PR = preorbital process; PT = postorbital process; SC = supraorbital crest; SR = sphenopterotic ridge; SS = suborbital shelf.

concentrate its prey before swallowing it'' (Taylor et al. 1983, p. 109).

Although the exact details of feeding behavior in the megamouth shark await observations on a live, feeding specimen, additional inferences can be made from morphological observations on the first two specimens. It is apparent that our earlier scenario (Taylor et al. 1983) was unduly influenced by the known feeding habits of the basking shark, which has often been seen and photographed swimming with mouth agape at the surface (Davis 1983; Stevens 1987). The strong swimming basking shark can efficiently pass a large volume of water through its pharynx and swallow part of its own bow wave along with the copepods and other invertebrate prey scattered in it. However, the weak body musculature, soft fins, restricted internal gill openings, and jaw morphology of the megamouth shark do not facilitate efficient feeding by this method. The megamouth shark might tend to shove water and prey ahead of it because water could not pass at any great rate between the densely packed papillose gill rakers and through the relatively small internal gill openings.

The slender jaws of the basking shark are hardly protrusible but swing ventrally on the cranium and spread laterally like a hoop, stiffening the almost circular mouth like the frame of a butterfly net (Fig. 11B), while the pharynx, hyobranchial arches and gill raker denticles are depressed and distended ventrolaterally. The heavy, long jaws of *Megachasma pelagios* are probably not widely distensible laterally, but, as shown by the Oahu and Catalina specimens, are highly protrusible anteriorly (Fig. 11A). The Catalina specimen, preserved with jaws maximally protruded, has its hyoid arch reversed in direction, with the hyomandibulae and ceratohyals anteroventral to their normal positions. This depresses the tongue, basihyobranchial skeleton and pharynx ventrally. The goblin shark, *Mitsukurina owstoni*, shows a similar hyoid reversal and pharyngeal depression when its jaws are protruded far forward (Fig. 11C).

Taylor et al. (1983) suggested that the megamouth shark had a bioluminescent mouth but could not prove it because of the poor preservation of the Oahu specimen. Sections of the black skin from the lower lip and tongue of the

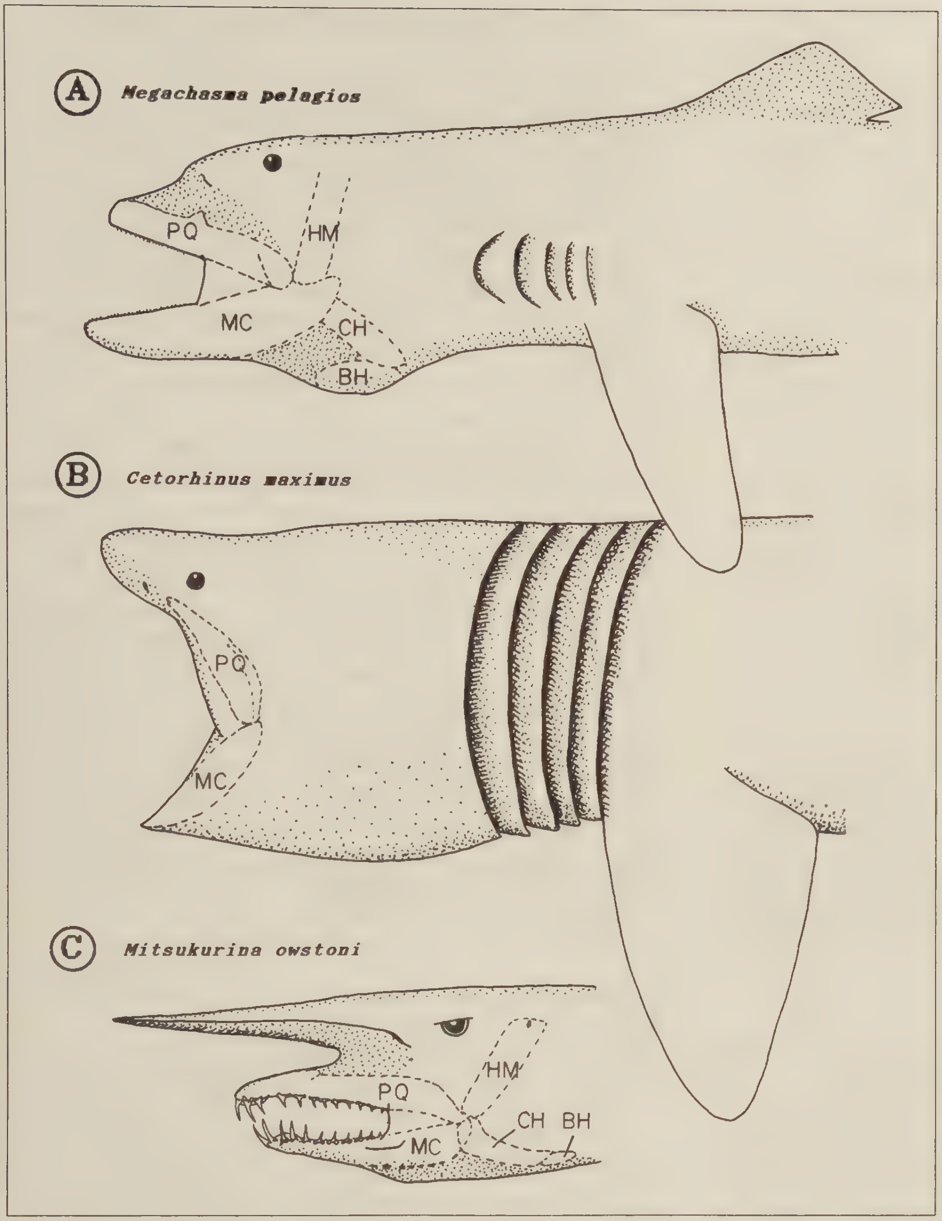

Figure 11.
Jaw mobility in the megamouth, basking, and goblin sharks. A, *Megachasma pelagios* (top) head with jaws protruded anteroventrally and hyoid arch reversed, composite of LACM-43745-1 and BPBM-22730. B, *Cetorhinus maximus* (center) head with jaws and hyobranchial arches distended lateroventrally in feeding posture but with jaws not protruded, composite of LACM-35593-1 and photos of feeding basking sharks in Davis (1983) and Stevens (1987). *C, Mitsukurina owstoni*, prebranchial head with jaws protruded and hyoid arch reversed as in the megamouth shark, composite of SU-13888 and RUSI-6206. ABBREVIATIONS: BH = basihyal; CH = ceratohyal; HM = hyomandibula; MC = Meckel's cartilage; PQ = palatoquadrte.

better preserved Catalina specimen revealed possible luminescent tissue (J. A. Seigel, Natural History Museum of Los Angeles County, Los Angeles, CA, pers. commun., 1985), along with iridescent, reflective upper jaw tissue (Taylor et al. 1983; Lavenberg and Seigel 1985). The nature of the lower jaw tissue may be resolved by investigations on the recently caught Australian specimen. Diamond (1985) discussed the use of a reflective, luminescent mouth to the megamouth shark as a "light trap" to attract its prey.

The above observations suggest a revised scenario for the feeding of the megamouth shark that is consistent with its feeding apparatus and its probable sluggishness. The megamouth shark can be imagined as slowly swimming through aggregations of euphausiid shrimp and other prey or floating in such aggregations with its jaws retracted and mouth open (Fig. 12A). If luminescent tissue is present on the upper jaw, the luminous, reflective tissue may be attractive to potential prey when producing light, and may serve to concentrate its near the mouth and jaws of the shark. Suddenly the megamouth shark protrudes its jaws, which reverses and depresses its hyoid arch, drops its tongue and pharynx, greatly increases the volume of its pharynx, and, like a gigantic bellows or underwater slurp gun, sucks the prey inside (Fig. 12B). The megamouth shark then closes its mouth and retracts its jaws; this action raises the pharynx and huge tongue, decreases the pharyngeal volume, and expels the water out through its closely screened internal gill openings (Fig. 12C). The shark swallows its food, opens its mouth again, and waits

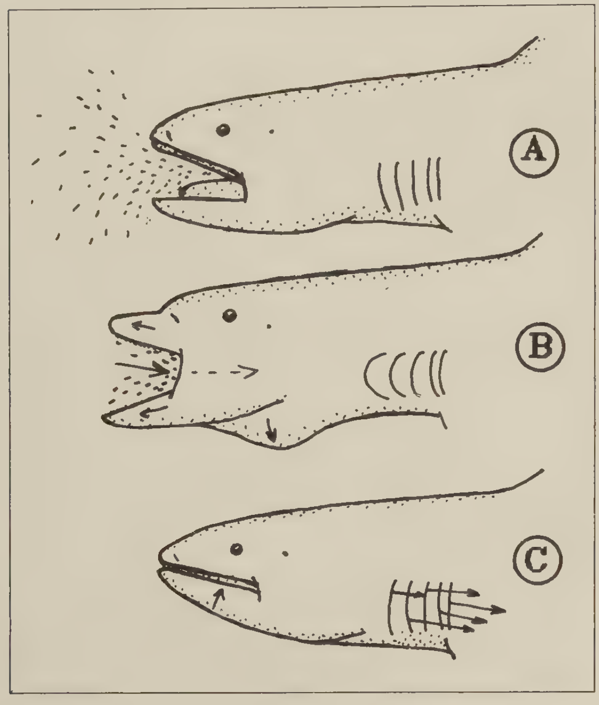

Figure 12.
Sequence of feeding action in *Megachasma pelagios*, based on the first two specimens. A, Mouth open with jaw retracted (top), luminescent organs would attract prey if present. B, Jaws protruded, hyoid arch reversed, and pharynx depressed, sucking prey into mouth. C, Mouth closed, hyoid arch and pharynx lifted, expelling water from gills. For further explanation see text.

for more victims to concentrate around its mouth, or slowly swims elsewhere to locate undisturbed patches of prey.

This scenario is not dependent on luminescent organs being present in *Megachasma*, because it may be able to feed on prey concentrations without their possible attractive effect. However the megachasmid feeding mechanism would be enhanced by a luminous oral lure. The extreme size of the jaws, the long pharynx, the *Mitsukurina*-like hyoid reversal, and the unusual cranial morphology of *Megachasma*, which permits the upper jaws to tuck in under the cranium, are apparent adaptations to producing a relatively large increase of pharyngeal volume and sudden inward flow of water when the shark protrudes its jaws.

Megachasma may have evolved its distinctive feeding apparatus from an odontaspidlike primitive jaw mechanism by exaggerating its jaw size and acquiring papillose gill rakers while harnessing and modifying the primitive lamnoid mode of jaw protrusion for suction-feeding. The basking shark, in contrast, could have evolved its feeding apparatus from a lamnidlike antecedent with restricted protrusion, but virtually eliminated protrusion in favor of jaw distension and a teleostlike method of filter feeding that is unparalleled amongst chondrichthyans.

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Appendix: Comparative Material of Lamnoid Taxa

Abbreviations for catalog or other numbers of lamnoid specimens examined in this study follow Leviton et al. (1985) and Compagno (1988):

BPBM—Bernice P. Bishop Museum, Honolulu, Hawaii
CAS—California Academy of Sciences, San Francisco
ISH—Institut für Seefischerei, Hamburg
LACM—Natural History Museum of Los Angeles County
LJVC-nnnn (e.g., LJVC-0251)— L.J.V. Compagno cataloged collection
LJVC-nnnnnn (LJVC-year/month/day, e.g., LJVC-840208)—L.J.V. Compagno field number;
MCZ—Museum of Comparative Zoology—Harvard

ORI—Oceanographic Research Institute, Durban
PEM—Field number of Port Elizabeth Museum, South Africa
RUSI—J.L.B. Smith Institute of Ichthyology
SOSC—Smithsonian Oceanographic Sorting Center
SU—Stanford University fish collection, now housed at CAS
USNM—United States National Museum of Natural History, Washington, D.C.

Mitsukurinidae: *Mitsukurina owstoni*

South Africa—RUSI-6206, 1166 mm immature female, Western Cape, west of Cape Town.

Japan—SU-13888, 1130 mm immature female (cranium dissected), Sagami Sea; USNM-50972, 335 cm adult female, skeleton, near Kosu, Sagami Bay.

Odontaspididae: *Carcharias taurus*

Western Atlantic—CAS 1961-IX:21, 1200 mm immature male and 1540 mm immature female (cranium and jaws removed from latter), no data.

South Africa—LJVC-831113, 1265 mm immature female, skeleton, Eastern Cape, Sardinia Bay; LJVC-840108, 2215 mm adolescent male, cranium, Eastern Cape; LJVC-840108, 2455 mm adolescent male, cranium, Eastern Cape; LJVC-840123, ~2.5 m adult male, cranium, Eastern Cape; LJVC-851228, 2250 mm adolescent female, Eastern Cape; LJVC-870103, 2200 mm adolescent female, jaws, Eastern Cape; LJVC-870805, 995 mm term fetus, skeleton, Natal; RUSI-27025, 1236 mm immature male, Algoa Bay.

Japan—MCZ-1278, 920 mm term fetus, Sagami Sea, HOLOTYPE of *Carcharias owstoni* Garman, 1913.

Odontaspis ferox

California—CAS-27022, ~3.2 m adult, cranium; CAS-27023, 1600 mm immature male, San Onofre; LJVC-0272, 2740 mm adult male, skeleton, San Clemente Island.

Hawaiian Islands—BPBM-9334 and BPBM-9335, 297 cm, heads only, both from Oahu, off Barber's Point.

South Africa—RUSI-6234, 1114 mm immature female, Natal.

Odontaspis noronhai

Dried jaw, possibly from Seychelles Islands, from D. J. Ward.

Pseudocarchariidae: *Pseudocarcharias kamoharai*

Central Atlantic—ISH-587, one female fetus, 415 mm, and 3 males, 397, 390, and 407 mm, from 1.1 m female, lat 12°07′N, long. 23°08′W.

South Africa—RUSI-6205 (ORI-1745), 930 mm adolescent female, lat. 33°29′S, long. 16°43′E, northwest of Cape Town; LJVC-880921, 972 mm adult male, Western Cape, washed up on beach, Blouberry Strand.

East Africa—RUSI-6181, 871 mm adult male, RUSI-6210, 970 mm adult male, longlined near Zanzibar(?).

Central Pacific—BPBM-18043, 823 mm adult male, lat. 20°02′N, long. 154°39′W, off Hawaii, Hawaiian Islands; CAS-32482, 933 mm adult male, lat 20°10′N, long 154°39′W, off Hawaii, Hawaiian Islands; RV *Charles H. Gilbert* 101-37, 955 mm female, lat. 21°20′N, long. 158°26′W, west of Oahu, Hawaiian Islands; RV *Townsend Cromwell* Cruise 44, Stn. 18, lat. 11°53′N, long. 144°49′W; LACM-uncat., 732 mm PCL immature female and 1100 mm adult male, both from lat. 7°33′S, long. 129°45′W, near Marquesas Islands.

Megachasmidae: *Megachasma pelagios*

BPBM-22730, 4460 mm adult male (dissected), off Oahu, Hawaiian Islands, HOLOTYPE of *Megachasma pelagios* Taylor, Compagno, and Struhsaker, 1983; LACM-43745-1, 4488 mm adult male, off Catalina Island, California. Possible megachasmid teeth, undescribed taxon: LACM-VP-10353, two teeth from Jewett Sand, Pyramid Hill, Kern Co., California, Miocene (Arikareean).

Cetorhinidae: *Cetorhinus maximus*

CAS-1953-IX: 23, dried jaws and gill rakers; LACM-35593-1, 7010 mm adult male, cranium, claspers, and other skeletal parts, off Avila Beach; LACM-42649-1, 5640 mm female, cranium and other parts, off San Pedro.

Alopiidae: *Alopias pelagicus*

Eastern Pacific—LJVC-0171, 1913 mm immature spec., cranium, Mazatlan, Mexico; LJVC-0414, 1970 mm immature male, cranium and other parts, lat. 11°53′N, long. 103°21′W; SIO-H52-19-5A, 560 male fetus and 585 female fetus, Galapagos Islands, off Fernandina.

South Africa—LJVC-870806, 3180 mm adolescent male, skeleton, Natal; LJVC-871125, 3330 mm adolescent female, cranium, jaws, vertebrae, Natal; RUSI-6247, 277 cm immature female, Natal, Durban.

Northern Indian Ocean—SOSC 79, RV *Anton Bruun* Cruise 5, near Stn. 282, 1372 mm immature female, lat. 16°14.5′N, long. 63°27′E, north Indian Ocean; SOSC 79, RV *Anton Bruun* Cruise 5, Stn. 288, 475 mm male fetus and 515 mm female fetus, lat. 9°36′N, long. 55°00′E, north Indian Ocean; SOSC 79, RV *Anton Bruun* Cruise 5, near Stn. 289, 727 mm female fetus, 3 male fetuses 660, 670, and 705 mm, lat. 7°17′N, long. 55°00′E, north Indian Ocean.

Taiwan—SU-21252, 614 mm male fetus, Takao.

Japan—SU-23415, 385 mm male fetus, Misaki.

Alopias superciliosus

Eastern Pacific—CAS-27072, 3715 mm adult male, off San Clemente Island; LJVC-0355, 2872 mm immature male, cranium and other skeletal parts, east-central Pacific, lat. 03°16′S, long 128°18′W; S.P. Applegate uncat., cranium, no data.

Florida—S. Gruber uncat., 2 male fetuses, one cleared and stained, 207 and 213 mm, from adult taken off Miami, Florida.

South Africa—RUSI-6248, 363 cm adult male, parts, Natal, Durban; PEM-790603, 4285 mm adult female, Eastern Cape, off Cape Recife.

Alopias vulpinus

California—S.P. Applegate uncat., 1308 mm immature male, cranium, S. California, Manhattan Beach Pier; S.P. Applegate uncat., cranium, (?)locality; CAS-30830, 1445 mm immature female, skeleton, San Francisco Bay; LACM-35592-1, 3099 mm female, head only, Los Angeles, Santa Monica Bay; LJVC-0234, 2057 mm immature female, cranium, Muir Beach; LJVC-0382, 1605 mm immature female, skeleton, Moss Landing; LJVC-0387, 1555 mm immature male, skeleton, Morton's Beach near Half Moon Bay; LJVC-0388, 1472 mm immature female, skeleton, Monterey Bay, Manressa State Beach near Rio Delmar; LJVC-0404, 1500 mm immature male, jaws, vertebrae, Moss Landing; LJVC-0473, 4200 mm adult male, cranium and claspers; LJVC-0474, 3700 mm immature female, cranium; SU-40908, 1752 mm immature female, no data.

South Africa—RUSI-8654, 3480 mm female, Eastern Cape, off Port Alfred; RUSI-26219 (LJVC-870130), 2022 mm immature male, Eastern Cape, off Port Alfred; LJVC-880229, 2882 mm adolescent male, Mossel Bay; RUSI-27024 (LJVC-870228), 2236 mm immature female, head and vertebrae, Langebaan, Saldanha Bay.

Lamnidae: *Carcharodon carcharias*

California—CAS-uncat., from J. D. McCosker, 1670 mm immature male, skeleton, Bodega Bay; CAS-53045, 1460 mm immature male, Ventura, off Ventura Marina; LJVC-0187, 2045 mm immature female, cranium, jaws, Tomales Bay near Inverness; LJVC-0261, 2340 immature male, cranium, Half Moon Bay; LJVC-0384, 1990 mm immature female, cranium, gill arches, jaws, fins, Half Moon Bay; LJVC-0475, 1290 mm immature male, cranium, jaws, gill arches, claspers, Baja California; LJVC-0478, 393 cm adult male, claspers, Año Nuevo; LJVC-0481, 4597 mm adult male, claspers, southeast of Anacapa Island; LJVC-0483, 5334 mm, cranium, Santa Cruz Island.

South Africa—LJVC-841026, 3058 mm immature female, cranium, Eastern Cape, Algoa Bay, Bird Island; LJVC-840126, 2000 mm immature male, Eastern Cape, Algoa Bay; LJVC-850226, 1585 mm immature male, Eastern Cape, Algoa Bay, Bird Island; PEM-801005, 2150 mm, New Brighton Beach, jaws only; LJVC-860502, 1510 mm immature male, Ciskei, Mgwalama; LJVC-860618, 2375 mm immature female, cranium, Eastern Cape, Algoa Bay; Gans Bay Fisheries Cooperative (LJVC-870303), 6000 mm female, jaws, fins, vertebrae, W. Cape, Gans Bay; LJVC-870805, 3027 mm immature female, cranium, vertebrae, Natal, Brighton Beach; LJVC-870830, 3826 mm adult male, cranium, vertebrae, teeth, fins, W. Cape, Koeberg; LJVC-871126, 2 adolescent males, 2830 and 2935 mm, crania and vertebrae, Natal; RUSI-12998, 1400 mm immature male, Algoa Bay; RUSI-6253, 1788 mm immature female, Natal, Umhlanga Rocks.

Isurus oxyrinchus

California—S.P. Applegate uncat., cranium, no data, S. California; LJVC-0216, 1360 mm immature female, cranium, jaws, vertebrae, off San Diego.

South Africa—LJVC-820816, 2330 mm adolescent female, cranium, jaws, vertebrae, Eastern Cape; LJVC-840122, 1982 mm immature female, cranium, jaws, vertebrae, Eastern Cape; LJVC-840726, 1773 mm immature female, cranium and LJVC-850405, 1400 mm immature female, skeleton, Eastern Cape, off Cape Recife; LJVC-870211, 1600 mm immature male, cranium, vertebrae, Eastern Cape, off Cape Recife; LJVC-870416, 1650 mm immature male, cranium, vertebrae, Eastern Cape, off Cape Recife; LJVC-880221, 1060 mm immature female, Eastern Cape, off Cape Recife; LJVC-870805, 2750 mm adult male, cranium, claspers, Natal; LJVC-uncat., dried jaw from huge individual, est. 396 cm, Western Cape, off Cape Town; RUSI-6916, 101 cm male, RUSI-6917, 284 cm male, RUSI-6918, 130 cm male, RUSI-6919, 120 cm female, RUSI-6920, 123 cm male, RUSI-6921, 82 cm male, RUSI-6922, 102 cm male, and RUSI-6923, 78 cm male, all dried jaws from Natal.

Isurus paucus

Western North Atlantic—LJVC-880125/LFM-8, 1096 mm full-term fetal female, from J. G. Casey.

Japan—S.P. Applegate uncat., 2175 mm adult male, cranium, claspers, teeth, Tokyo Fish Market.

Central Pacific—USNM-197429, 1380 mm immature female, PARATYPE of *Isurus alatus* Garrick, 1967.

Lamna ditropis

California—LJVC-0112, 2280 mm adult male, cranium, jaws, vertebrae, claspers, Monterey Bay, off Monterey; LJVC-0113, 2200 mm female, cranium, jaws, vertebrae, Monterey Bay; LJVC-0385, 1829 mm immature male, cranium, gill arches, vertebrae, fins, off Pescadero; LJVC-0476, 2200 mm adult male, cranium, claspers, Monterey Bay, Monterey Canyon; LJVC-0477, adult male, head only, Monterey Bay, Monterey Canyon; LJVC-0494, ~1 m, jaws, vertebrae, Monterey area; LJVC-uncat., 983 mm immature male, Northern California.

Lamna nasus

Western North Atlantic—LJVC-880127, head of ~2m individual, from J. G. Casey.

Italy—B. Welton uncat., 2476 mm, tooth set, caught off Sicily.

Southern Indian Ocean—SOSC, RV *Anton Bruun* Cruise 5, Stn. 309, 960 mm immature female, lat. 42°23′S, long. 74°56′E.

Anacoracidae:
Squalicorax "falcatus" (? = *S. pristodontus*)

LACM-VP-16056, chondrocranium, jaw fragments, and teeth, Upper Cretaceous, Logan Co., Kansas.

Note: While this paper was in press, Nakaya (pers. commun., 1988; Nakaya 1989) reported a fourth magamouth shark (also an adult male over 4 m long) that was stranded on the beach at Hamamatsu City, Shizuoka Prefecture, south-central coast of Honshu, Japan (34°42′N, 137°42′E). This was photographed by beachgoers but was washed out to sea and lost before scientists were notified of its presence and could collect it.

A Morphometric Approach to Distinguish Between the Upper Dentitions of *Carcharhinus limbatus* and *C. brevipinna* with Comments on Its Application to Tracing Shark Phylogenies Through Their Fossil Teeth

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ABSTRACT

A morphometric analysis of upper tooth variation among 24 specimens of *Carcharhinus limbatus* and 18 specimens of *C. brevipinna* was carried out. Results from a Sheared Principal Components Analysis (S.P.C.A.) show that the two species can be clearly distinguished on the basis of their isolated teeth. It is suggested that all species that show less similarity in tooth form than the pair tested will be identifiable to species using S.P.C.A. It is proposed that S.P.C.A. be employed to trace *Carcharhinus* species lineages through their fossil tooth records.

Introduction

The reconstruction of evolutionary histories of taxa has been characterized by two basic approaches: 1) The direct retrieval of fossils that make up evolutionary lineages, and 2) The study of the distribution of traits among living groups of organisms, leading to inferences about their histories. A wealth of important evolutionary information is provided when both approaches are available for any one taxon. For example, inferred speciations can be dated (geologically), rates and modes of evolutionary change can be determined, and incidences of convergence and divergence can be documented. Unfortunately, the paleontological approach toward phylogenetic reconstruction has been markedly less fruitful than the inferential approach, a fact that is generally attributed to the poor fossil record of most taxa. As a result, little paleontological documentation exists for the inferred evolutionary histories of many taxa.

Sharks may be one group for which this imbalance between paleontological and inferential phylogenetic data may be redressed, as they are well represented as fossils, in the form of isolated teeth. Indeed, their fossil teeth may make sharks the best represented vertebrates in the entire fossil record (Maisey 1984a, b). The abundance of fossil teeth is attributable to the prolific rate of tooth replacement seen in sharks. A single individual, in the course of a lifetime, can produce and serially lose several thousand teeth (extrapolation based on the data of Moss [1967] and typical individual longevity). A small proportion of this perpetual shower of replaced teeth has become fossilized in marine coastal sediments to provide a relatively continuous and extensive documentation of their evolutionary history.

Of the many shark genera with good fossil records, the genus *Carcharhinus* stands out as one particularly well represented by extant taxa. Thirty extant species are currently recognized within the genus (Compagno 1988). The genus' distribution extends across tropical, subtropical, and temperate waters of the world. The first teeth that are assigned to *Carcharhinus* in the fossil record appear in the Eocene (Ward 1980). However, *Carcharhinus* is not well represented in the fossil record until the Miocene when it becomes abundant at localities in several parts of the world (Capetta 1987 and references therein).

Given the excellent fossil record for teeth of the genus *Carcharhinus* and the group's extant representation, it should be possible both to infer the group's evolution from character distributions among extant taxa and to track species lineages directly through the fossil record. In this paper I focus only on problems associated with tracking the group's evolution through the fossil record, and present

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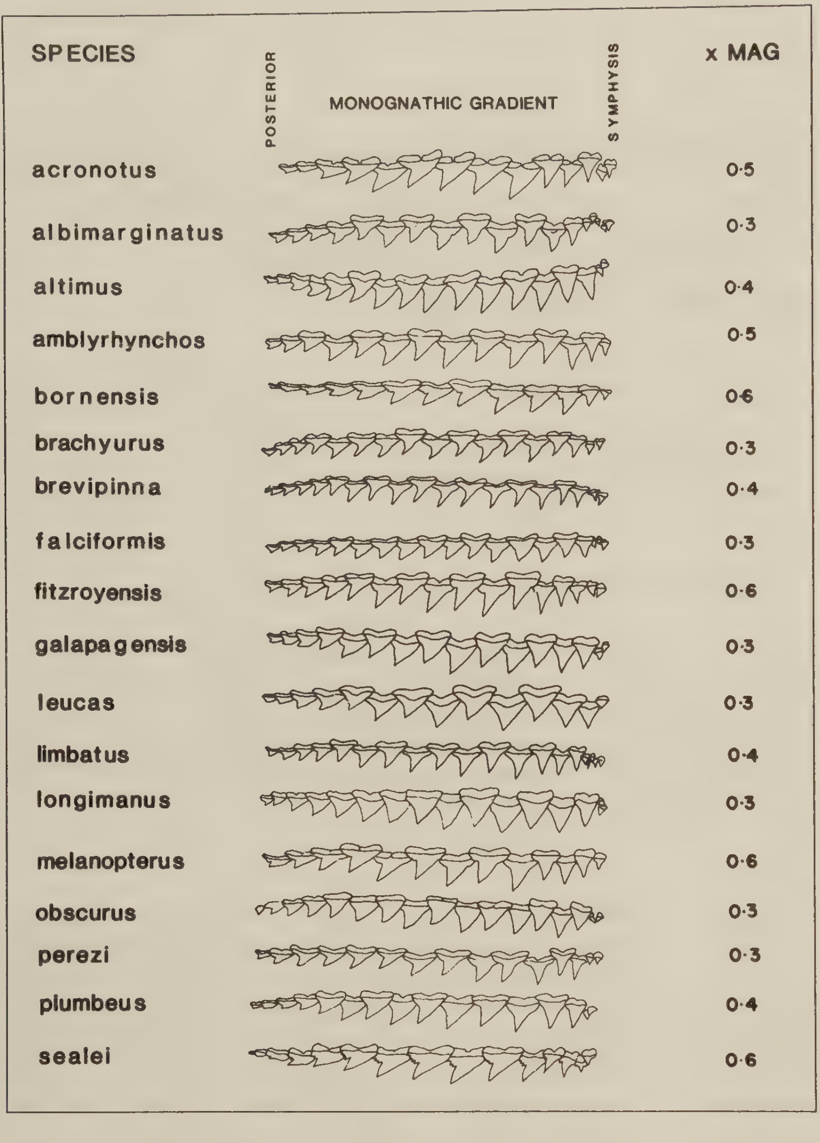
SPECIES
POSTERIOR
MONOGNATHIC GRADIENT
SYMPHYSIS
x MAG
acronotus 0·5
albimarginatus 0·3
altimus 0·4
amblyrhynchos 0·5
bornensis 0·6
brachyurus 0·3
brevipinna 0·4
falciformis 0·3
fitzroyensis 0·6
galapagensis 0·3
leucas 0·3
limbatus 0·4
longimanus 0·3
melanopterus 0·6
obscurus 0·3
perezi 0·3
plumbeus 0·4
sealei 0·6

Figure 1.
Gradient monognathic heterodonty in upper jaw teeth of adult *Carcharhinus*. Eighteen of thirty extant species are represented. All teeth shown are redrawn from Garrick (1982) and are representive of adult specimens. Approximate relative magnification is given for each species. Note the incrementally graded nature of tooth differences within jaw that serve to obscure among species differences in tooth form.

the results of an analysis that suggest it may be possible to identify isolated fossil teeth to species.

Background

Paleontologists have been unable to infer evolutionary pattern or phyletic change in tooth morphology from the extensive fossil record of *Carcharhinus* teeth because they have been unable to assign isolated fossil teeth to species with any degree of confidence. This has been due both to our incomplete knowledge of intraspecific tooth variation (due to dignathic and monognathic heterodonty, ontogenetic heterodonty, and sexual heterodonty), and to our lack of understanding of interspecific variation among living species of *Carcharhinus*. The situation has been made worse by the chaotic state of the systematics of living *Carcharhinus*, which was resolved only recently by Garrick's revision of the genus (Garrick 1982, 1985).

In order to better appreciate the problems associated with interspecific and intraspecific variation in fossil teeth, it is instructive to review the exact nature of comparable variation among extant species. Teeth of extant *Carcharhinus* show consistent differences between upper and lower jaws (dignathic heterodonty) and an incrementally graded change in shape and size from the front to the back of the jaw (gradient monognathic heterodonty). When the teeth of sharks from different species are compared (Fig. 1), it becomes clear that tooth position within the jaw accounts for as least as much of the overall tooth shape variation as does the interspecific component. In fact this gradient monognathic variation is so dramatic that back teeth of different species superficially resemble one another more than they do the front teeth of conspecifics. It is likely then,

Table 1.
Material of *Carcharhinus* examined.

Species	Size (cm TL)	Sex	Location
C. limbatus	170	F	Gulf of Mexico (Alabama coast)
	167	F	Gulf of Mexico (Alabama coast)
	161	F	Gulf of Mexico (Alabama coast)
	161	?	Gulf of Mexico (Alabama coast)
	150	F	Gulf of Mexico (Alabama coast)
	148	M	Carribean Sea (Belize)
	139	M	Gulf of Guinea (Sierra Leone coast)
	127	F	Gulf of Mexico (Alabama coast)
	127	M	Gulf of Mexico (Alabama coast)
	118	M	Gulf of Mexico (Alabama coast)
	117	M	Gulf of Mexico (Alabama coast)
	112	M	Gulf of Mexico (Alabama coast)
	108	M	Gulf of Mexico (Alabama coast)
	106	M	Gulf of Guinea (Sierra Leone coast)
	100	M	Gulf of Guinea (Sierra Leone coast)
	96	M	Gulf of Guinea (Sierra Leone coast)
	96	M	Gulf of Mexico (Alabama coast)
	92	F	Gulf of Guinea (Sierra Leone coast)
	91	M	Gulf of Guinea (Sierra Leone coast)
	89	F	Gulf of Guinea (Sierra Leone coast)
	89	M	Gulf of Guinea (Sierra Leone coast)
	87	M	Gulf of Guinea (Sierra Leone coast)
	81	F	Gulf of Guinea (Sierra Leone coast)
	?	F	Western Atlantic (Jacksonville, Florida)
C. brevipinna	233	F	Gulf of Guinea (Sierra Leone coast)
	212	F	Gulf of Mexico (Alabama coast)
	202	F	Gulf of Mexico (Alabama coast)
	191	F	Gulf of Mexico (Alabama coast)
	177	F	Gulf of Mexico (Alabama coast)
	177	M	Gulf of Mexico (Alabama coast)
	176	F	Gulf of Mexico (Florida coast)
	170	F	Gulf of Mexico (Alabama coast)
	163	F	Gulf of Mexico (Alabama coast)
	150	F	Gulf of Mexico (Alabama coast)
	98	F	Gulf of Mexico (Alabama coast)
	97	M	Gulf of Guinea (Sierra Leone coast)
	95	F	Gulf of Mexico (Alabama coast)
	95	M	Gulf of Mexico (Alabama coast)
	94	M	Gulf of Guinea (Sierra Leone coast)
	85	F	Gulf of Guinea (Sierra Leone coast)
	85	M	Gulf of Guinea (Sierra Leone coast)
	83	F	Gulf of Guinea (Sierra Leone coast)

that this monognathic gradient is the main source of variance that confounds species identification and thus prevents researchers from assigning fossil teeth to species lineages with confidence. However, it should be noted that ontogenetic variation and sexual dimorphism in tooth form can also contribute extensively to the confounding of species identification from teeth (Raschi et al. 1982).

While gradient monognathic variation in *Carcharhinus* is great, it is also highly structured. This can be seen at a glance by noting how tooth crowns become incrementally lower and more recurved toward the posterior of the jaw (Fig. 1). If this structured variation could be accounted for and "eliminated", then any species differences, previously obscured by monognathic variation, would become apparent. A technique that can be adapted to do precisely this is the Sheared Principal Component Analysis (S.P.C.A.) of Bookstein et al. (1985). Essentially S.P.C.A. employs regression analysis to remove within-group trends. A Principal Components Analysis of the residuals, after the within-group variance has been removed by regression, then represents variance that is not confounded with within-group effects. If S.P.C.A. proves to be an effective method to eliminate monognathic variation and thus reveals interspecific differences in extant *Carcharhinus* teeth, then it might subsequently be applied to fossil teeth to ascertain their species identity and so permit reconstruction of fossil species lineages.

Materials and Methods

The hypothesis that the elimination of structured monognathic variation allows species-specific differences to be made apparent was tested. Dried jaws of *C. limbatus* and *C. brevipinna* were chosen to represent the pair of species in the genus *Carcharhinus* least likely to be distinguished from one another on the basis of tooth shape alone (Fig. 1). In order to represent all possible forms of intra-specific variation and thus rigorously to test the idea that species-specific traits exist on isolated teeth, the teeth of ontogenetic variants of both sexes from distinct populations were included in the sample of teeth for each species (Table 1). A sample of 642 upper jaw teeth were removed from 18 specimens of *C. brevipinna* and from 24 specimens of *C. limbatus*. Both species were represented by samples predominantly from Sierra Leone, West Africa and from the Gulf of Mexico (Table 1).

Representative teeth were collected by soaking each jaw in warm water until teeth became loose. Teeth were then removed, labelled, and placed in a sequential jaw map to reflect their natural positions in the jaw, following D'Aubrey (1964). Teeth were extracted and measured from the second row only. These teeth were chosen because they were fully formed and were in perfect condition. Homologous points (Fig. 2) were then assigned for all teeth and recorded on a video-digitizing system. Twenty-one (21) homologous distances were subsequently computed from these coordinate data (Fig. 2). These 21 distance variables and one variable representing tooth position in the jaw were first subjected to a (standard) Principal Components Analysis to summarize the extent of total variation between species, within species, and within jaw. The same data set was subsequently subjected to a Sheared Principal Components Analysis, "sheared" to eliminate the effect of monognathic variation.

Results

The standard Principal Component Analysis plot of P.C. 1 vs. P.C. 2 showed almost no cluster separation between species (Fig. 3). The Sheared Principal Components Analysis plot of residuals (after monognathic heterodonty effects had been removed by regression), S.P.C. 1 vs. S.P.C. 2, showed a discrete cluster of points that represented only the teeth of *C. limbatus* and two loose subclusters corresponding to juveniles and adult specimens of *C. brevipinna* (Fig. 4).

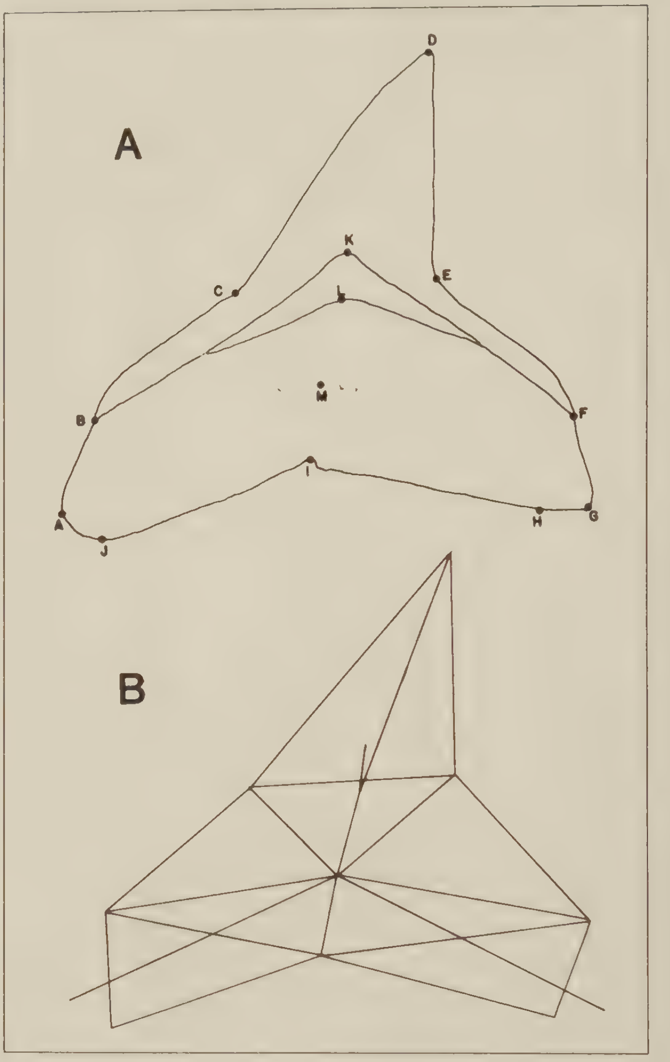

Figure 2.
A, Typical *Carcharhinus* tooth shown with "homologous" landmarks used for this study. B, Distance variables computed with an automated video-digitizer from "homologous" points represented above (Fig. 2A).

Discussion

The results of the standard Principal Components Analysis attest to the extent to which teeth of these two species cannot be distinguished from one another when all sources of variance are included in analysis.

By contrast, the Sheared P.C.A. shows very different results. Most striking is the fact that only a few points appear on the plot in spite of there being 642 teeth used in the analysis (cf. Fig. 3). This is due to the fact that a quadratic regression accounted for so much of the monognathic variation that residuals about the regression appeared as single points rather than clusters when plotted in Principal Component space. In biological terms this is a reflection of the very high degree to which monognathic

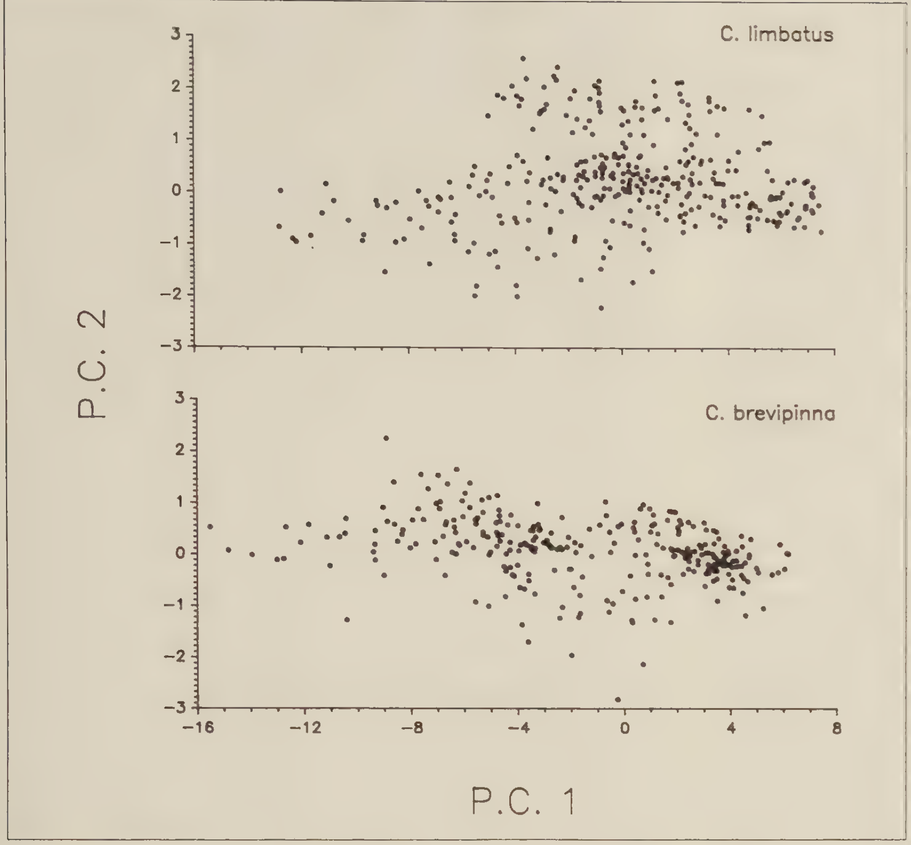

Figure 3.
Plots of Principal Component 1 against Principal Component 2 for 642 upper jaw teeth. Teeth from 18 specimens of *C. brevipinna* are represented on the lower plot while teeth from 24 specimens of *C. limbatus* are represented in the upper plot. Note that the cloud clusters occupied by the two species are, for practical purposes, indistinguishable.

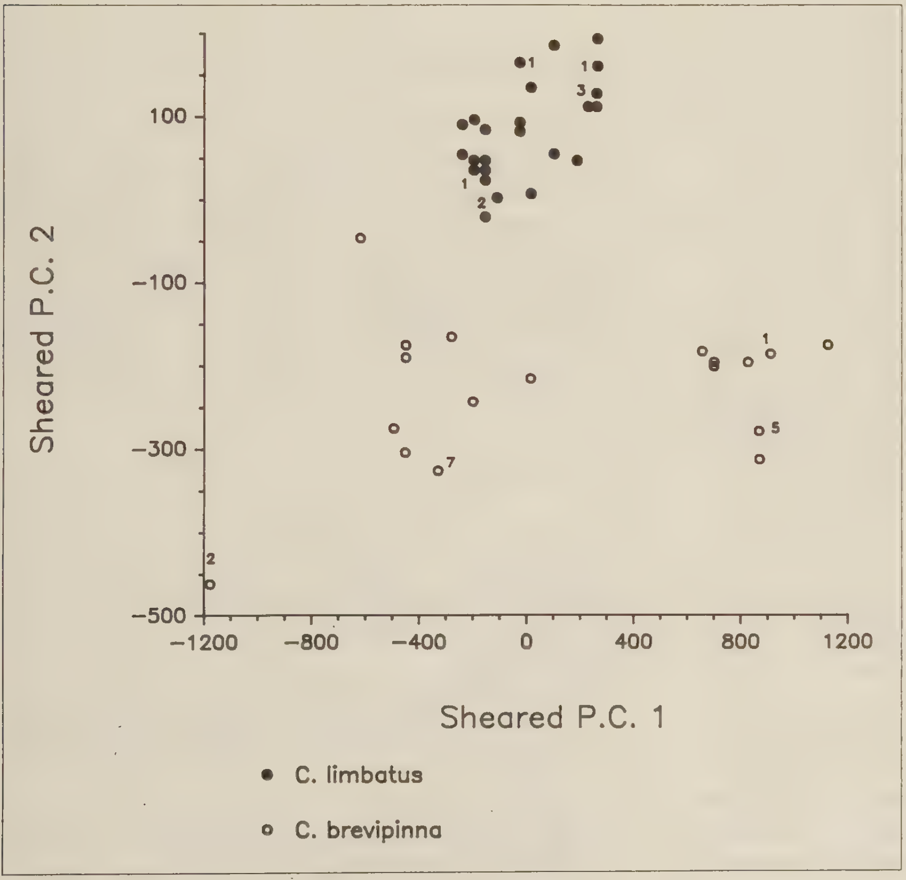

Figure 4.
Plot of Sheared Principal Component 1 against Sheared Principal Component 2 for the same data represented in Figure 3. Within jaw variation has been statistically removed using a quadratic regression. Each circle (open for *C. brevipinna* closed for *C. limbatus*) represents the position of 10 or more superimposed teeth from the same jaw. Each integer represents the number of teeth present if less than 10.

gradient heterodonty is structured. Each point on the sheared plot marks the position of 10 or more superimposed teeth from the same jaw. Each integer represents the number of teeth present, if less than 10, at any one point.

The second and more important point is that, once the confounding within-jaw variation has been removed by regression, the two species separate into discrete clusters. Thus all the *C. limbatus* teeth are grouped together in a cluster that is quite distinct from the *C. brevipinna* cluster. This is a remarkable finding, given the apparent similarity of the teeth between *C. brevipinna* and *C. limbatus* and the extent of the intraspecific variants used in the test (see Table 1). While the *C. limbatus* teeth form a tight cluster in this analysis the *C. brevipinna* teeth appear to be represented as two subclusters. This is a consequence of having two discrete size categories, juveniles and adults, represented in the *C. brevipinna* sample. A more even representation of all size classes would probably have linked together the subclusters. However, the striking nature of the subclusters may be somewhat misleadingly represented. As more species are included in the analysis, the morphospace occupied by teeth expands (to accommodate the new species shapes added). This affects pre-existing clusters by making them appear tighter, because they occupy a smaller proportion of the plotted area. Thus, subclusters within single species should present problems only to species identification when within-species cluster variation is greater than among-species cluster variation.

These results indicate that teeth can be identified to species for two species that exhibit very similar tooth morphologies and suggest that more marked separation will be seen when teeth from species with more trenchant tooth morphology differences are studied. The fact that isolated teeth of extant sharks exhibit species specific traits has exciting implications. For if fossil teeth also exhibit species specific traits and if the monognathic trends in fossil teeth can be similarly removed using S.P.C.A., then it will be possible to trace species lineages through the fossil record. (The assertion that it might be possible to remove the monognathic contribution to variation in fossil teeth is based on the assumption that fossil members of the genus exhibit the same monognathic trends as do their extant descendants. This assumption can be validated by noting that all extant members of the genus show similar monognathic clines (eighteen of which can be seen in Figure 1). If fossil members of the genus exhibited a different monognathic trend, it would be necessary to invoke convergence toward the same kind of clinal monognathic heterodonty in 30 different extant taxa. (There is no reason to invoke such an assertion.)

In order for this clear species separation (Fig. 4) to be achieved using S.P.C.A. (Fig. 3), the position of each tooth had to be included as a variable. This presents a problem if a similar analysis is to be used for fossil teeth, because jaw positions of isolated teeth are not immediately apparent. However, the observation among extant species of uniform monognathic clinal trends (Fig. 1) suggests that there may exist position-specific variables in teeth that are common to all species of the genus *Carcharhinus*. Preliminary (unpublished) data based on a discriminant analysis by tooth position across nine species lend support to this supposition but cannot be regarded as conclusive, because the sample size used to represent each species varied between 2 and 19 owing to the limited availability of some material. (The analysis was therefore strongly biased toward determining tooth position for those species that were best represented in the sample.) Data collection for a more robust and extensive test of this hypothesis, using 20 representatives of 11 different species within the genus, is currently in progress. The degree to which the position of an isolated tooth can be accurately and objectively ascertained will be of pivotal importance in tracing the evolution of sharks through the fossil record, because it will determine the extent to which isolated fossil teeth can be identified to species. If fossil teeth can be identified to discrete species clusters, the changes seen in those clusters over time (at successive geological horizons) should reflect the evolution of the species lineage under study.

If it is indeed possible to identify fossil teeth to species using S. P. C. A. then it may be feasible, for the first time, to interpret and piece together what is arguably the richest fossil record of any vertebrate group.

Acknowledgments

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Summary of Records of the Deep-Water Skates, *Raja* (*Amblyraja*) *badia* Garman, 1899 and *Bathyraja abyssicola* (Gilbert, 1896), in the Eastern North Pacific

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Synopsis

Zorzi and Anderson (1988) redescribed the deep-water skates, *Raja* (*Amblyraja*) *badia* Garman, 1899 and *Bathyraja abyssicola* (Gilbert, 1896), on the basis of their examination of eleven specimens from off California. They reported new records, including the first California records of *R. badia*, and range extensions for both species. They also provided data on external morphological characters, counts, and measurements, and corrected some errors in the literature. The results of this study were presented at the U.S.-Japan Workshop on Elasmobranchs as Living Resources, and are summarized here.

The broad skate, *Raja badia*, was recorded in the eastern Pacific from seven known specimens, from off central Panama north to Vancouver Island, British Columbia, collected at depths of 1280–2322 m. Additionally, two morphologically similar specimens were noted from the western Pacific off northern Japan.

R. badia was described as a medium-sized *Raja*, to 985 mm TL; disc rhomboid, width 1.3 times disc length; dorsal surface of disc and tail covered with prickles; rostrum with greatly enlarged thornlets in a random pattern; one pair each of preorbital, postorbital, and interspiracular thorns; two or three pairs of scapular thorns; continuous row of 24–29 thorns along midline of body and tail; tail short, with row of enlarged thornlets on either side of median thorns; ventral surface of disc and tail completely smooth. Dorsal coloration medium gray-brown to dark gray; numerous darker spots and blotches, especially toward apices of disc; conspicuous brown bar across scapular region. Ventral coloration same, with whitish blotches on snout and upper abdomen, and margins of nares, nasal curtain, mouth, gill slits, and cloaca. Sexual maturity of males was reported to occur at approximately 900 mm TL.

The deep-sea skate, *Bathyraja abyssicola*, was recorded in the eastern Pacific from 14 extant specimens, from West Cortes Basin, California, north to the Queen Charlotte Islands, British Columbia. It was also recorded in the western Pacific from eight specimens, from off central Honshu Island, Japan, north to the Bering Sea. Specimens of *B. abyssicola* have been collected at depths of 362–2903 m.

B. abyssicola was described as a large *Bathyraja*, to 1350 mm TL; disc bell-shaped, slightly broader than long; orbit length equal to interorbital distance; both surfaces of disc and tail covered with minute denticles; one to five median nuchal thorns separated from a continuous row of median thorns on trunk and tail. Dorsal coloration uniform, light gray to dark chocolate brown. Ventral coloration same or slightly darker; distal margins of disc and tail darker; whitish around mouth, posterior edges of labial folds, gill slit distal margins, and cloacal opening; tips of pelvic fin anterior lobes and tips of claspers whitish. Males with large, irregular whitish blotches, often with numerous dark spots, on abdomen; greatly reduced or, more usually, completely absent in females. Juveniles were reported to be more dorsoventrally depressed; tail length, dorsal and caudal fin bases ontogenetically longer; denticles absent from abdominal region and ventral surface of pelvic fin anterior lobe. Sexual maturity of males was reported to occur at approximately 1100 mm TL.

We note a rather intriguing similarity in the way our knowledge of both *R. badia* and *B. abyssicola* has unfolded. The type specimen of each was collected during the early 1890's from eastern Pacific locations by the U.S. Fish Commission steamer *Albatross*, using a large beam trawl. No additional specimens of either were collected until the 1960s; even today, the number of known specimens remains low. While nearly all of these specimens were collected by fishery research vessels using bottom trawls, at least one specimen of each was collected in a commercial sablefish trap. Both have been recorded from a relatively great range in the eastern Pacific, with either conspecific or very closely related examples reported from the western Pacific.

Their original descriptions, published in the late 1890's and based on only a single specimen of each, were sufficiently complete and accurate to avoid synonymic confusion in subsequent literature. Until the 1980s, however, references in the literature were either based on the original description, limited to brief descriptions or citations in checklists and keys, or confined to merely recording the capture of additional specimens. The first really "new" information on these fishes was based on recent studies of western Pacific specimens. Nakaya (1983) published photographs and brief descriptions of two specimens from off northern Japan (listed as *Raja* sp.), which appeared morphologically indistinct from eastern Pacific specimens of *R. badia*. Dolganov (1983) and Ishihara and Ishiyama (1985) provided detailed descriptions and drawings of crania and claspers of western Pacific *B. abyssicola*.

Since our draft was submitted (June 1987), additional data for both *R. badia* and *B. abyssicola* have been made available. Ishihara (Department of Fisheries, Faculty of Agriculture, University of Tokyo, pers. comm., Dec. 1987) confirmed the conspecificity of the Japanese skates listed as *Raja* sp. by Nakaya (1983) with eastern Pacific *R. badia*. He also informed us of a 23rd specimen of *B. abyssicola*, MTUF 26068, an adult male collected July 1987, in 500 m off Tanaga Island, Aleutian Islands, at lat. 51°31′30″N, long. 178°06′42″W. This find greatly strengthens our conclusion that the range of *B. abyssicola*, a eurybathic, slope-dwelling species, appears to be continuous from at least California to Japan. Interestingly, this specimen did not exhibit the large white abdominal blotches noted on male specimens from off California examined by us.

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Shark Exploitation and Conservation

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ABSTRACT

The magnitude, distribution, and nature of world fisheries for sharks and other cartilaginous fishes is detailed for the postwar period from 1947 to 1985, using statistics published by the Food and Agriculture Organization of the United Nations. Catches in this period have tripled, particularly mirroring postwar development of chondrichthyan fisheries in Third World countries. The species of sharks utilized for fisheries are indicated for the thirty families of sharks, and shark species are ranked by importance to fisheries. The problems with exploitation of sharks and other chondrichthyans are discussed, and recommendations made for their conservation.

Introduction

Sharks and other cartilaginous fishes are not taken in the vast weights reported for commercially important bony fishes such as scombroids, clupeoids, and gadoids, but still the yearly nominal world catch of mixed chondrichthyans is currently running over 600,000 metric tons (mt) per year (Food and Agriculture Organization of the United Nations [FAO] 1986). The present review of world fisheries for sharks, and perforce for other cartilaginous fishes when cumulative world statistics are considered, was written at the behest of the organizers of the United States–Japan Workshop on Elasmobranchs as Living Resources held in Honolulu, Hawaii, in December 1987.

Data and Methods

The present analysis of world fisheries for sharks and other cartilaginous fishes relies in part on the nominal catch-weight statistics published by FAO, as well as qualitative data on sharks accumulated by various FAO projects (Compagno and Vergara 1978; Compagno 1981a, 1984a, b). The statistics are derived from the annual FAO Yearbook of Fishery Statistics (FAO 1953–1986), and cover the years 1947 through 1985. The FAO Yearbook for 1986 had not been published when this manuscript was submitted (April 1988) and data from it is not included in this paper.

Limits of FAO Fishery Statistics

There are considerable difficulties in extracting and interpreting cartilaginous fish statistics from the FAO yearbooks, in part because the arrangement of data and kinds of data presented by the FAO compilers has varied over the years, and has been retrospectively corrected and modified for the past three to six years in successive yearbooks. Additionally, several countries that routinely report fisheries data on cartilaginous fishes to FAO at present, did not do so thirty years ago, while others have changed the type of data supplied to FAO. Some countries have reported data on major fisheries for cartilaginous fishes throughout the period covered by the yearbooks (e.g., Japan, the United Kingdom, France, and Norway), while some that currently land large catches of chondrichthyans had miniscule and unimportant catches twenty or more years ago (e.g., the U.S.S.R., Brazil, Mexico, Nigeria, India, Pakistan, and Sri Lanka).

Politics has apparently played an important role in the availability of fisheries statistics to FAO. Several countries that currently conduct important fisheries for sharks and other cartilaginous fishes did not exist when the U.N. and FAO were formed, and far fewer countries are represented in early FAO yearbooks than in those of the last two decades. Political problems may have influenced the availability of fisheries statistics from certain important chondrichthyan-fishing countries during parts of the postwar period, particularly Taiwan and the People's Republic of China.

Although some countries represented in the FAO yearbooks present their catch data as separate statistics for sharks, rays, and chimaeras, and may further distinguish statistics for a small number of shark species such as the porbeagle, *Lamna nasus*, and piked dogfish, *Squalus acanthias*, many place all sharks in a single category, place sharks and rays together, or include all cartilaginous fishes together. This makes it difficult to determine the worldwide cumulative catch statistics for sharks or for individual shark species that are important to fisheries but are not reported routinely in the FAO yearbooks. Indeed, the only worldwide chondrichthyan statistic consistently presented over the entire history of the FAO Yearbook of Fishery Statistics is the cumulative world catch of chondrichthyans.

Some developed countries in Western Europe have regularly supplied cumulative chondrichthyan statistics as well as separate catch data for sharks, rays, and chimaeras, and catch data for a few important species. This is not the case for most nations now or in the past. FAO has a vigorous program which has published numerous taxonomic field guides to the marine fisheries species of different countries and to the FAO fisheries statistical areas, as well as taxonomic catalogs of groups of marine organisms of importance to fisheries. This program is intended to increase the taxonomic diversity of fisheries statistics and may eventually produce statistics for many species of cartilaginous fishes that are currently lumped in aggregate categories.

Estimates from published national catches in the last 20 years of the FAO Yearbooks suggest that shark catches are at least equal to batoid catches and may exceed them by up to 2:1. Kreuzer and Ahmed (1978) estimated the 1976 world shark catch to be 307,085 mt, about 55% of that year's catch of approximately 556,000 mt of mixed chondrichthyans. The catch for chimaeroids is probably less than 1% of elasmobranch catches, and consists primarily of elephant fishes (family Callorhinchidae, *Callorhinchus* spp.), caught off Australia, New Zealand, South America, and southern Africa.

There are numerous difficulties in compiling a database on world fisheries of sharks and other cartilaginous fishes. Apart from political turmoil which may prevent data collection in developing countries, many nations with limited numbers of trained fisheries officers face the daunting task of monitoring numerous and scattered small-scale fisheries and offshore international fishing fleets. Research priorities on fisheries species in such countries may be needed for certain marine teleosts showing far larger and more valuable catches than chondrichthyans of all species. Fisheries workers may have great difficulties in identifying species of cartilaginous fishes and other fisheries species in many areas.

The FAO data for nominal catches of cartilaginous fishes probably represents only a minimal figure for the actual world catch, and should be considered as a relative index of trends in world chondrichthyan and shark catches. The FAO statistics are for *nominal catches* of fishes and refer to *live weights*, including both conversions from processed weights of various fish products, and gutted, eviscerated, filleted, dried, and salted fish, as well as fishmeal, oil, etc. The FAO nominal catches of chondrichthyans may very well represent only a partial, although major, fraction of actual catches. Cartilaginous fishes are routinely caught, killed, and discarded as a bycatch of major offshore fisheries that target more valuable marine teleosts, and such bycatches are not included in FAO fishery statistics. Sports anglers catch cartilaginous fishes in considerable numbers in some countries, and their catches are also not included in FAO statistics. Such processed chondrichthyan products as dried shark fins, mixed fish meal made from chondrichthyans and teleosts, and liver oil may be difficult to monitor and to accurately convert to whole-weight nominal catch statistics.

A few small, "negative" fisheries for chondrichthyans also exist, essentially predator-control programs to eliminate undesirable chondrichthyans that interfere with human activities, and which are normally not included in international fisheries statistics. The chondrichthyans caught in such fisheries are generally not utilized or cost more to catch than any possible profit from their utilization. The most well-publicized of these programs are shark-netting operations off Australia and South Africa, which exist essentially to protect swimmers at bathing beaches by killing potentially dangerous sharks in their proximity.

Methodology

Data were extracted for nominal catches of sharks and of all cartilaginous fishes for the entire four-decade period (1947–1985) covered by the yearbooks. For comparison with world chondrichthyan catches nominal catch data were extracted for the following: all fisheries organisms (freshwater and marine) reported by FAO, and three of the most important major teleost fisheries groups, the clupeoid, scombroid and gadoid fishes. Catch data were also extracted for the most important FAO statistical areas (Fig. 1) for chondrichthyan catches. Nominal catch data were extracted mostly for countries with "major" fisheries for cartilaginous fishes, those which generally take upwards of 10,000 mt of chondrichthyans per year. Finally, when possible, catch data were extracted for individual shark species and higher taxonomic groups of sharks.

World Catches

World chondrichthyan catches have increased approximately threefold from 1947 to 1985, from 200,000 to 600,000 mt (Table 1), with a possible leveling trend in the early 1980s. Total world catches of fisheries species in the

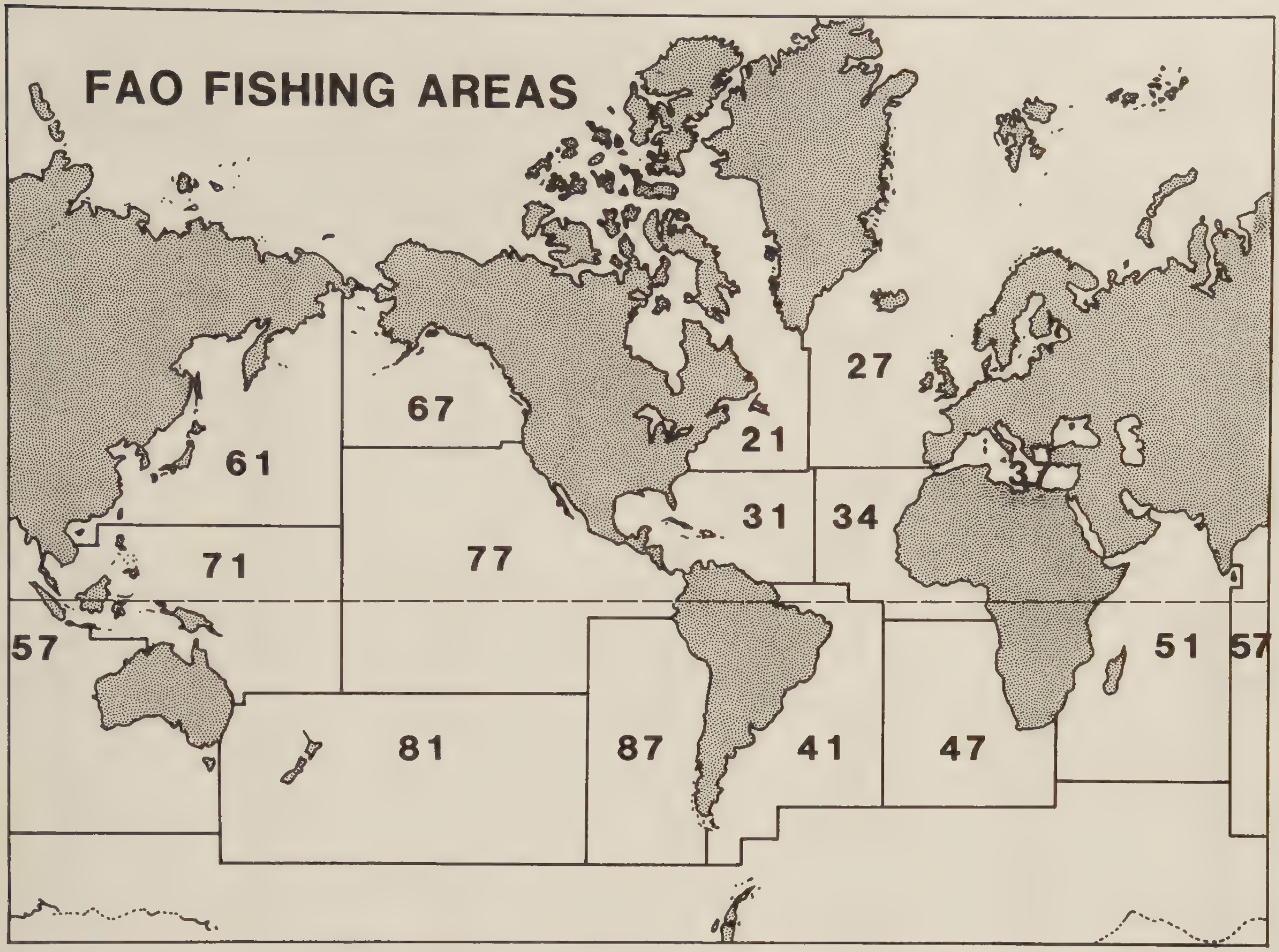

Figure 1.
World map in Mercator projection showing principal FAO Fishery Areas where cartilaginous fishes are caught: Area 21, Western North Atlantic; 31, Western North-Central Atlantic; 41, Western South-Central Atlantic; 27, Eastern North Atlantic and part of Arctic Ocean; 34, North-Central Atlantic; 37, Mediterranean Sea; 47, Eastern South Atlantic; 51, Western Indian Ocean; 57, Eastern Indian Ocean; 61, Western North Pacific; 71, Western Central Pacific; 81, Western South Pacific; 67, Eastern North Pacific; 77, Eastern North-Central Pacific; and 87, Eastern South Pacific.

same period showed an approximately fourfold increase (Table 1), with no apparent leveling. Chondrichthyan catches have varied from about 0.7 to 1.2% of world fisheries in the postwar period, with irregular fluctuations from 1950 to the 1980s. Clupeoid, scombroid, and gadoid catches show fivefold to sixfold increases (Table 1) in the same period, with gadoid and scombroid catches leveling off in the late 70s. Clupeoids show a dramatic increase and recovery in catches in the late 70s and 80s after a precipitous crash in the early 70s due to decline of anchoveta, *Engraulis ringens*, fisheries off Peru and Chile. Catches of sharks and other chondrichthyans have assumed a lesser importance in the past forty years relative to clupeoids, gadoids, and particularly scombroids (Table 2).

The number of individual chondrichthyans taken yearly in the world catch is obviously very large, but only an educated guess of this number is possible with the FAO statistics. If the average individual weight of the cartilaginous fishes caught from 1975 to 1985 equaled the weight of an average human being (68 kg or 150 lb), the world chondrichthyan catch in this period, averaging 596,000 mt per year, would include approximately 8.8 million individuals per year. Probably a more reasonable average weight per individual chondrichthyan, judging from the average maximum total length of sharks (Compagno 1981b, about 1.5 m) and from knowledge of maximum sizes of rays and chimaeras, would be roughly 10 kg, and a more reasonable estimate for the number of individuals caught worldwide would be 60 million per year.

Table 1.

Nominal world catches of Chondrichthyes and estimated shark catches compared to other fishery species and to total world catches, from FAO Yearbook of Fishery Statistics, 1947–1985. Sharks estimated at 55% of the total nominal chondrichthyan catch. Catches in thousands of mt.

	Chondrichthyes		Important teleosts			
Year	Total	Sharks	Clupeoids	Scombroids	Gadoids	Total catch
1947	201	111	3481	534	2892	20000
1948	211	116	3486	507	2862	19600
1949	245	135	3724	611	2951	20100
1950	204	112	4081	726	2793	21100
1951	197	108	4392	724	2996	23600
1952	203	112	5440	1320	2900	25200
1953	204	112	5500	1200	2730	25900
1954	194	107	5760	1340	2860	27600
1955	270	149	6410	1530	3960	28900
1956	280	154	7020	1700	4170	30500
1957	310	171	7230	1820	3780	31500
1958	300	165	7450	1980	3650	32800
1959	300	165	9060	2000	3830	36400
1960	320	176	10290	2130	4100	39500
1961	370	204	12620	2190	5040	43000
1962	380	209	14730	2310	5540	46400
1963	400	220	14930	2430	5910	47600
1964	400	220	18730	2651	6060	52000
1965	405	223	17442	2884	6794	52400
1966	433	238	19426	3350	7309	57300
1967	444	244	20308	4093	8350	60400
1968	476	262	21117	4452	9617	63900
1969	502	276	18786	4657	9941	62700
1970	480	264	22209	4757	10535	70352
1971	482	265	20241	4876	10681	70707
1972	466	256	14288	4885	11472	66121
1973	589	324	12073	5417	11970	62824
1974	544	299	14631	5736	12699	66597
1975	571	314	14373	5560	11882	66487
1976	556	306	15371	5673	12130	69870
1977	563	310	13043	6249	10595	69170
1978	590	325	14493	7285	10409	70548
1979	599	329	15790	7422	10610	71287
1980	616	339	16070	7265	10757	72089
1981	629	346	17566	6614	10650	74840
1982	631	347	18539	6638	10974	76763
1983	586	322	18146	6610	11219	77257
1984	607	334	20425	7393	12252	83096
1985	607	334	21943	6868	12408	84945
Mean:	419	231	13092	3753	7494	51829

Catches by Oceans and FAO Fishing Areas

The FAO yearbooks subdivide nominal chondrichthyan catches and other catch statistics by broad geographic subdivisions of the earth's surface as well as by country. Up to the mid-60s, categories of broad continental and political boundaries were used (Africa, Asia, Europe, North and South America, U.S.S.R., and Oceania) but for the last twenty years a numbered system of FAO Major Fishing Areas for Statistical Purposes was substituted which reflects the modern increase in pelagic fishing operations well beyond continental coastlines and political boundaries. Twenty years of data (1965 to 1985) on chondrichthyan catches from the principal FAO Areas in which chondrichthyans are caught (Fig. 1) are included in Table 3. Catch data for these Areas are combined for entire oceans and their subdivisions (Table 4) as follows: Atlantic and Mediterranean Sea (Areas 21, 27, 31, 34, 34, 41, and 47); Indian Ocean (Areas 51 and 57); and Pacific (Areas 61, 67, 71, 77, 81, and 87).

Table 2.
World catches of Chondrichthyes compared to catches of clupeoid, scombroid and gadoid fishes, 1947–1985. Data from FAO yearbooks. Chondrichthyes (CH), clupeoid (CL), scombroid (SC), and gadoid (GA) catches rendered as percentages of total world fisheries catches (TC), and chondrichthyan catches rendered as percentages of clupeoid, scombroid, and gadoid catches.

	Group catches as % of world catches				Chondrichthyes as % of major teleost catches		
Year	CH%TC	CL%TC	SC%TC	GA%TC	CH%CL	CH%SC	CH%GA
1947	1.0	17.4	2.7	14.4	5.8	37.6	7.0
1948	1.1	17.7	2.6	14.6	6.1	41.6	7.4
1949	1.2	18.5	3.0	14.6	6.6	40.0	8.3
1950	1.0	19.3	3.4	13.2	5.0	28.0	7.3
1951	0.8	18.6	3.1	12.6	4.5	27.2	6.6
1952	0.8	21.5	5.2	11.5	3.7	15.3	7.0
1953	0.8	21.2	4.6	10.5	3.7	17.0	7.5
1954	0.7	20.8	4.9	10.3	3.4	14.4	6.8
1955	0.9	22.1	5.3	13.7	4.2	17.6	6.8
1956	0.9	23.0	5.6	13.6	4.0	16.4	6.7
1957	1.0	22.9	5.8	12.0	4.3	17.0	8.2
1958	0.9	22.7	6.0	11.1	4.0	15.1	8.2
1959	0.8	24.8	5.5	10.5	3.3	15.0	7.8
1960	0.8	26.0	5.4	10.3	3.1	15.0	7.8
1961	0.9	29.3	5.1	11.7	2.9	16.8	7.3
1962	0.8	31.7	5.0	11.9	2.6	16.4	6.9
1963	0.8	31.3	5.1	12.4	2.7	16.4	6.8
1964	0.8	36.0	5.1	11.6	2.1	15.0	6.6
1965	0.8	33.2	5.5	12.9	2.3	14.0	6.0
1966	0.8	33.9	5.8	12.7	2.2	12.9	5.9
1967	0.7	33.6	6.8	13.8	2.2	10.8	5.3
1968	0.7	33.0	7.0	15.0	2.3	10.6	4.9
1969	0.8	29.9	7.4	15.8	2.7	10.7	5.0
1970	0.7	31.5	6.8	14.9	2.2	10.0	4.6
1971	0.7	28.6	6.9	15.1	2.4	9.9	4.5
1972	0.7	21.6	7.4	17.3	3.3	9.5	4.1
1973	0.9	19.2	8.6	19.0	4.9	10.8	4.9
1974	0.8	21.9	8.6	19.0	3.7	9.5	4.3
1975	0.9	21.6	8.4	17.8	4.0	10.2	4.8
1976	0.8	21.9	8.1	17.3	3.6	9.8	4.6
1977	0.8	18.8	9.0	15.3	4.3	9.0	5.3
1978	0.8	20.5	10.3	14.7	4.1	8.1	5.7
1979	0.8	22.1	10.4	14.8	3.8	8.1	5.6
1980	0.9	22.2	10.0	14.9	3.8	8.5	5.7
1981	0.8	23.4	8.8	14.2	3.6	9.5	5.9
1982	0.8	24.1	8.6	14.2	3.4	9.5	5.7
1983	0.8	23.4	8.6	14.5	3.2	8.9	5.2
1984	0.7	24.5	8.9	14.7	3.0	8.2	5.0
1985	0.7	25.8	8.1	14.6	2.8	8.8	4.9
Mean:	0.8	24.6	6.5	13.9	3.6	15.1	6.1

The Pacific Ocean (Fig. 2) has had steady and continuing growth in chondrichthyan catches while the Atlantic–Mediterranean peaked in the late 60s and early 70s, declined in the mid-70s and recovered in the mid-80s. The Indian Ocean catches peaked in the early 70s, declined and hit a plateau through the early 80s, and declined again by the mid 80s. Catches of chondrichthyans in the Pacific were about 78% of Atlantic catches in 1965 but equaled them in 1985. Indian Ocean catches were about half the Atlantic catches in 1965 and 1985 but peaked in 1973 at about 77% of Atlantic catches.

In the Western Atlantic (Fig. 3), catches in Area 21 (western North Atlantic) peaked in the mid-70s and then sharply declined, while catches for Area 31 (western North-Central Atlantic) and Area 41 (western South-Central Atlantic) steadily increased in importance and overtook Area 21 in the late 1970s. Area 21 produced slightly more than Area 31 and about half of the catch of Area 41 in 1965. The catch for Area 21 subsequently increased fivefold to peak in 1975, then dropped ninefold to a low in 1978, and recovered in 1985 to about half its peak catch. In 1985 catches from Area 31 was slightly more than those from

Table 3.

World nominal chondrichthyan catches listed by FAO fishery areas, 1965–1985. Data from FAO yearbooks. Catches in thousands of mt. Abbreviations: WNA, Western North Atlantic (21); ENA, Eastern North Atlantic (27); WCA, Western Central Atlantic (31); ECA, Eastern Central Atlantic (34); MED, Mediterranean Sea (37); WSA, Western South Atlantic (41); ESA, Eastern South Atlantic (47); WIN, Western Indian Ocean (51); EIN, Eastern Indian Ocean (57); WNP, Western North Pacific (61); ENP, Eastern North Pacific (67); WCP, Western Central Pacific (71); ECP, Eastern Central Pacific (77); WSP, Western South Pacific (81); ESP, Eastern South Pacific (87)

	Atlantic Ocean and Mediterranean Sea							Indian Ocean		Pacific Ocean					
Year	WNA 21	ENA 27	WCA 31	ECA 34	MED 37	WSA 41	ESA 47	WIN 51	EIN 57	WNP 61	ENP 67	WCP 71	ECP 77	WSP 81	ESP 87
1965	11.0	107.8	9.4	14.1	16.2	19.3	3.7	57.9	27.4	80.2	2.2	23.8	12.8	10.6	8.6
1966	16.2	107.1	9.8	14.6	16.3	20.3	8.5	73.6	26.0	77.6	2.1	27.2	10.2	12.1	11.6
1967	10.0	116.7	10.5	8.3	23.9	29.0	6.5	78.2	20.6	77.9	1.7	16.8	12.8	9.7	21.2
1968	19.0	114.2	10.9	12.4	19.4	30.8	7.0	75.1	24.4	97.0	1.5	23.8	10.0	4.3	25.9
1969	26.0	127.7	10.0	16.1	18.8	24.4	7.5	81.4	29.2	100.5	1.3	28.9	10.7	3.7	15.8
1970	15.7	111.6	6.4	47.3	12.5	23.8	6.8	75.4	31.8	103.8	1.0	31.6	13.7	4.4	19.9
1971	37.1	100.7	7.0	52.8	16.3	25.4	4.7	80.8	29.2	98.3	0.5	30.8	12.3	6.1	12.8
1972	39.6	104.3	8.1	36.2	10.3	16.2	7.6	117.2	27.9	94.9	0.4	32.2	12.5	4.6	12.8
1973	36.1	100.6	10.2	30.2	9.8	31.2	7.1	153.9	20.8	98.9	5.5	44.7	16.6	5.9	23.6
1974	40.1	92.1	10.9	38.3	11.2	26.4	5.2	95.1	43.9	104.1	2.3	45.1	17.2	5.8	18.1
1975	49.3	98.5	11.4	42.7	12.6	27.0	3.7	95.2	39.5	124.4	1.9	52.5	14.8	6.2	15.6
1976	29.8	89.9	11.7	36.7	13.9	19.9	2.5	97.4	37.3	122.0	3.9	53.1	17.4	8.3	12.0
1977	14.6	83.1	14.1	35.3	13.7	19.4	5.1	116.7	33.4	123.5	5.3	55.8	19.2	8.6	16.5
1978	7.9	91.8	11.8	39.9	13.3	24.7	17.7	126.1	34.2	107.7	6.6	62.8	22.4	6.9	16.3
1979	11.3	88.8	10.3	40.7	24.8	22.4	8.7	123.6	33.5	106.4	9.9	56.6	26.5	7.5	14.9
1980	11.1	82.9	14.0	47.3	16.9	37.2	4.9	113.0	42.4	113.2	10.1	64.5	27.8	10.9	19.2
1981	12.7	83.2	19.9	45.9	18.1	35.6	7.4	114.9	47.3	101.5	5.0	69.0	33.2	11.7	23.5
1982	10.1	76.8	20.3	46.4	21.5	45.8	7.6	119.1	42.5	102.7	5.3	66.8	32.6	12.3	21.4
1983	12.0	87.0	24.7	47.2	23.9	40.3	6.4	71.3	47.0	99.1	5.6	65.4	25.1	13.3	17.8
1984	10.0	87.7	27.9	37.4	25.4	38.5	5.6	69.0	47.4	99.8	5.3	71.0	28.4	15.6	37.6
1985	22.6	90.1	25.1	31.2	24.6	42.9	5.4	81.7	48.7	97.9	4.6	71.0	26.7	14.7	19.8
Mean:	21.0	97.3	13.5	34.3	17.3	28.5	6.6	96.0	34.9	101.4	3.9	47.3	19.1	8.7	18.3

Area 21, while Area 41 had almost double the catch of Area 21.

In the Eastern Atlantic and Mediterranean (Fig. 4) Area 27 (eastern North Atlantic and southern Arctic Ocean) remained far more productive than Areas 34 (eastern North-Central Atlantic), 37 (eastern South Atlantic), and 47 (Mediterranean Sea) combined, but catches from the area have gradually declined after a peak in 1969. Catches from Area 34 rose to a peak in 1971 but leveled off, while Area 47 had a low and mostly level production. Area 37 showed only limited fluctuations and a slight decline in catches during the first seven years and a slight increase in the last thirteen years of the period 1965 to 1985.

The Indian Ocean (Fig. 5) catches have had massive fluctuations, which may indicate overexploitation. In 1965, Area 51 (Western Indian Ocean) produced about twice the catch as Area 57 (Eastern Indian Ocean), then rose to eight times the Area 57 catch in 1973. The Area 51 catch then sharply dropped, leveled off, and dropped again to a level about half again as great as Area 57 in 1985. Area 57 rose slightly, by a third, with relatively slight fluctuations in the same period.

In the Western Pacific (Fig. 6) Area 61 (western North Pacific) dominated in catches and produced more than Area 71 (Western Central Pacific) and Area 81 (Western South Pacific) combined. This exactly mirrors the Eastern Atlantic and reflects the heavy chondrichthyan catches of Japan, South Korea, Taiwan, and China in their home waters, analogous to the large catches of the United Kingdom, Norway, France, and Spain in Area 27. Area 61 has consistently produced large catches, peaking in the late 70s and declining moderately towards 1985, but catches in Area 71 have increased from about 25% of Area 61 catches in 1965 to about 70% in 1985. As with Area 47 in the Eastern Atlantic, Area 81 has had low, relatively steady catches that are an eighth or less of those in Area 61. Area 81 catches increased slightly from 1972 through 1985.

In the Eastern Pacific (Fig. 7) Area 67 (eastern North Pacific) has generally produced much smaller chondrichthyan catches than Area 77 (eastern North-Central Pacific)

Table 4.
World nominal chondrichthyan catches listed by oceans and major subdivisions of oceans. Data from FAO yearbooks, 1965–1985. Catches in thousands of mt.

	Atlantic Ocean and Mediterranean Sea				Pacific Ocean		
Year	Western	Eastern	Total	Indian Ocean	Western	Eastern	Total
1965	39.7	141.8	181.5	85.3	114.6	23.6	138.2
1966	46.3	146.5	192.8	99.6	116.9	23.9	140.8
1967	49.5	155.4	204.9	98.8	104.4	35.7	140.1
1968	60.7	153.0	213.7	99.5	125.1	37.4	162.5
1969	60.4	170.1	230.5	110.6	133.1	27.8	160.9
1970	45.9	178.2	224.1	107.2	139.8	34.6	174.4
1971	69.5	174.5	244.0	110.0	135.2	25.6	160.8
1972	63.9	158.4	222.3	145.1	131.7	25.7	157.4
1973	77.5	147.7	225.2	174.7	149.5	45.7	195.2
1974	77.4	146.8	224.2	139.0	155.0	37.6	192.6
1975	87.7	157.5	245.2	134.7	183.1	32.3	215.4
1976	61.4	143.0	204.4	134.7	183.4	33.3	216.7
1977	48.1	137.2	185.3	150.1	187.9	41.0	228.9
1978	44.4	162.7	207.1	160.3	177.4	45.3	222.7
1979	44.0	163.0	207.0	157.1	170.5	51.3	221.8
1980	62.3	152.0	214.3	155.4	188.6	57.1	245.7
1981	68.2	154.6	222.8	162.2	182.2	61.7	243.9
1982	76.2	152.3	228.5	161.6	181.8	59.3	241.1
1983	77.0	164.5	241.5	118.3	177.8	48.5	226.3
1984	76.4	156.1	232.5	116.4	186.4	71.3	257.7
1985	90.6	151.3	241.9	130.4	183.6	51.1	234.7
Mean:	63.2	155.5	218.7	131.0	157.5	41.4	198.9

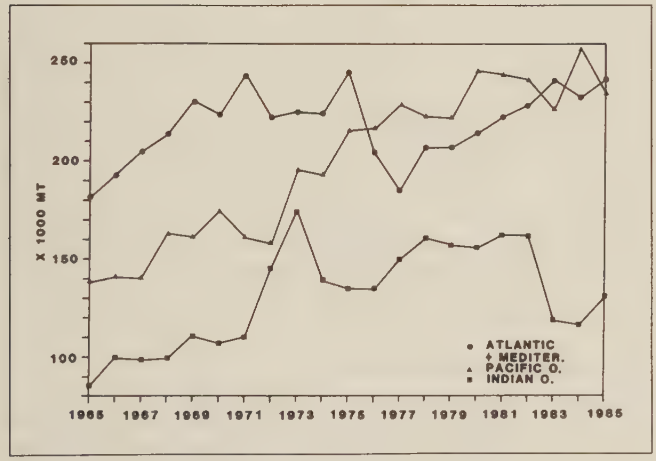

Figure 2.
Nominal catches of cartilaginous fishes in the Atlantic Ocean and Mediterranean Sea, the Indian Ocean, and the Pacific Ocean, 1967 to 1985.

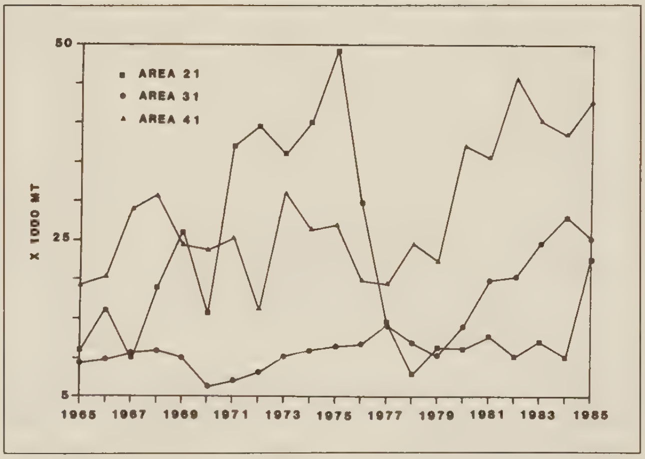

Figure 3.
Nominal catches of cartilaginous fishes in the Western Atlantic Ocean (FAO Areas 21, 31, and 41), 1967 to 1985.

and Area 87 (eastern South Pacific). Area 67 catches have shown a decline, bottoming in 1972 and increasing modestly until leveling out through 1985. Area 77 catches have doubled and Area 87 has tripled its catches from 1965 through 1985. Production may have fallen off in these areas in 1984 and 1985, but the variability of their yearly catches makes this uncertain.

Catches by Countries

Most maritime countries catch sharks and other cartilaginous fishes, but relatively few have major fisheries with over 10,000 mt landed yearly. Nominal catch records from 1947 to 1985 for nineteen of the most important chondrichthyan-fishing countries are presented in Table 5.

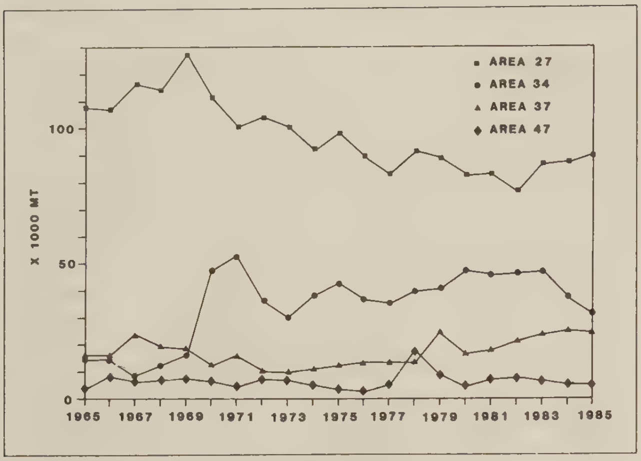

Figure 4.
Nominal catches of cartilaginous fishes in the Eastern Atlantic Ocean (FAO Areas 27, 34, 37, and 47) and Mediterranean Sea (Area 37), 1967 to 1985.

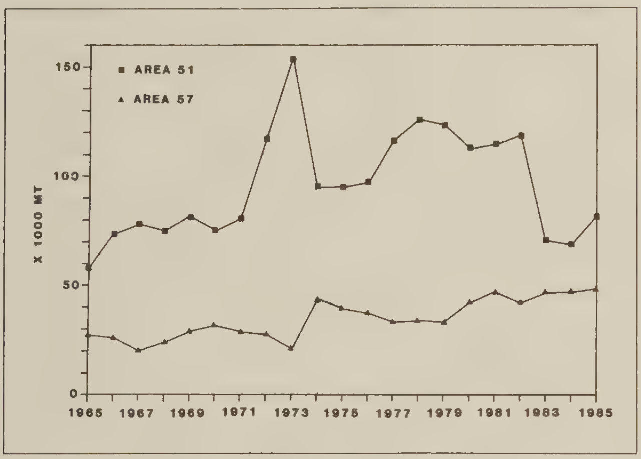

Figure 5.
Nominal catches of cartilaginous fishes in the Indian Ocean (FAO Areas 51 and 57) 1967 to 1985.

Notable omissions include the People's Republic of China and Taiwan, both of which take major catches of cartilaginous fishes. Catch statistics for these fishes are not reported in the FAO yearbooks for China, while such statistics were reported for Taiwan from 1953 to 1969 and subsequently dropped. Taiwan is one of the world's foremost fishing nations and continues to catch cartilaginous fishes in large numbers. A major component of the Taiwanese chondrichthyan fishery targets large and medium-sized sharks worldwide. These are caught for their fins which are made into sharkfin soup base, a product that has greatly increased in value in the past decade. Taiwanese chondrichthyan catches totaled 10,700 mt in 1953 and steadily rose to peak catches of 33,100 mt in 1968 and 32,700 mt in 1969, with a mean catch of 19,300 mt in the period from 1953 through 1969.

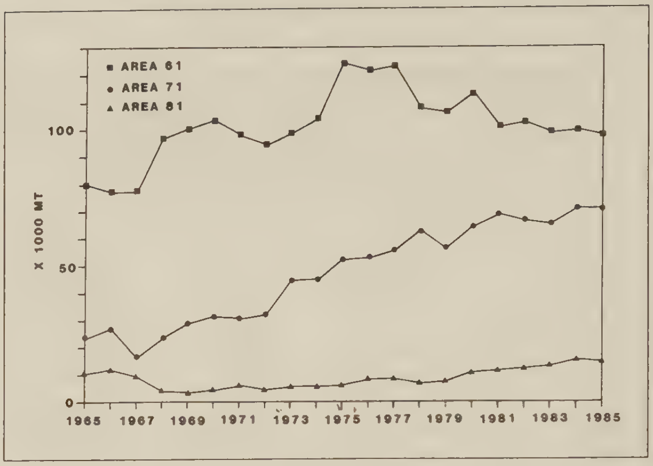

Figure 6.
Nominal catches of cartilaginous fishes in the Western Pacific Ocean (FAO Areas 61, 71, and 81), 1967 to 1985.

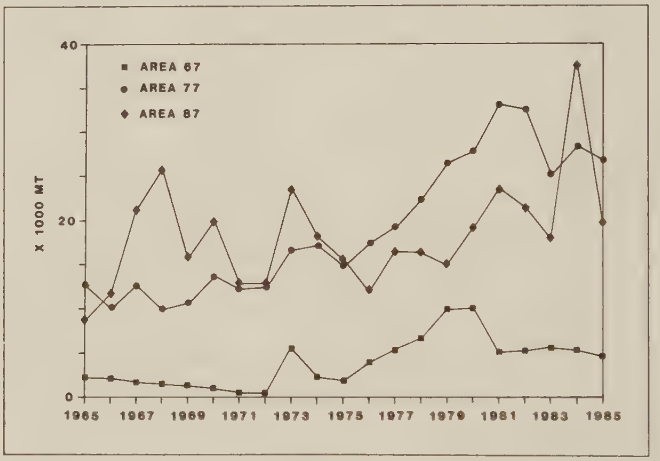

Figure 7.
Nominal catches of cartilaginous fishes in the Eastern Pacific Ocean (FAO Areas 67, 77, and 87), 1967 to 1985.

Western Hemisphere

In North America (Fig. 8), the United States has an irregular chondrichthyan catch record, reflecting peaks and declines in local fisheries and also changes in eating habits of the populace. From an early peak in the late 1940s U.S. catches declined markedly through the mid-1950s, then rose to a peak and plateau in the late 1950s. They declined markedly to a plateau in the 1960s, then dropped to a miniscule level in the early and mid-1970s. However, from 1976 to 1985, U.S. chondrichthyan catches rose dramatically and hit a plateau comparable to that of the 1950s. The early peak and decline may reflect the collapse of the West Coast fishery for shark liver oil and vitamin A extract (Roedel and Ripley 1950), with tope shark (soupfin shark, *Galeorhinus galeus*), piked dogfish (spiny dogfish or spurdog, *Squalus acanthias*), and bluntnose sevengill shark (*Notoryn-*

Table 5.
World nominal catches of selected countries with major chondrichthyan fisheries, 1947–1985. Data from FAO yearbooks. Mean catches calculated for entire period 1947 to 1985 for each country, except for those with starting year delimited at bottom of Table as "From". Catches in thousands of mt.

Year	USA	Mexico	Argentina	Brazil	Peru	USSR	UK	France	Norway	Spain	Nigeria	Indonesia	Malaysia	Japan	South Korea	Thailand	India	Pakistan	Sri Lanka
1947	13.1	0	6.9	0	1.0	0	27.1	20.5	10.8	10.4	0	0	0	73.2	0	1.0	0	0	0
1948	12.8	0	5.1	0	1.4	0	29.8	16.0	10.7	10.4	0	0	0	86.1	14.6	2.0	0	1.5	0
1949	11.2	0	2.4	0	1.2	0	30.7	16.7	10.0	10.6	0	0	0	118.5	0	3.0	0	9.1	0
1950	6.1	0	1.0	0	1.3	0	29.2	13.7	12.0	10.8	0	0	0	100.7	0	2.0	0	0	0
1951	12.8	0	1.2	0	1.1	0	32.6	13.5	14.0	11.6	0	0	0	85.7	0	2.0	0	0	0
1952	3.1	0	1.7	0	2.5	0	30.8	13.1	15.3	10.1	0	0	0	89.1	0	2.0	0	9.8	0.6
1953	2.0	0	2.9	0	3.0	0	28.8	14.4	15.5	10.8	0	0	0	97.4	10.5	2.2	15.9	10.8	0.7
1954	2.8	0	2.4	0	4.5	0	27.8	13.7	18.8	10.9	0	0	0	102.9	9.2	2.3	16.0	9.8	3.1
1955	2.8	0	2.2	0	0	0	28.6	14.9	19.1	10.8	0	0	0	97.2	10.8	1.6	20.4	11.7	2.5
1956	3.3	4.1	3.8	0	3.3	0	27.1	15.2	22.8	11.7	0	0	0	92.6	14.8	1.6	21.9	9.7	3.0
1957	14.3	4.5	4.1	0	3.5	0	29.1	15.2	20.9	14.1	0	0	0	93.8	12.2	3.1	23.1	17.6	3.9
1958	16.6	5.6	4.6	0	3.4	0	29.2	15.2	24.4	14.2	0	0	0	82.9	10.2	2.7	24.3	9.5	4.3
1959	16.6	4.6	4.0	4.6	4.2	0	27.2	15.1	22.0	15.4	0	0	0	86.0	7.6	2.8	23.5	9.8	4.3
1960	16.6	0	2.4	5.0	7.2	0	25.7	16.7	29.0	14.0	0	0	0	83.9	10.9	4.3	35.6	11.3	7.1
1961	5.7	3.6	2.9	5.9	3.8	0	27.8	34.3	45.6	14.3	0	0	3.2	78.3	8.7	4.0	33.6	9.4	8.5
1962	9.0	3.4	3.9	0	5.4	0	23.6	33.1	38.7	10.6	0	0	3.2	81.5	9.9	4.5	40.8	22.0	10.3
1963	9.0	3.5	6.2	7.6	5.1	0	23.5	35.5	51.6	11.4	0.3	0	4.4	77.4	9.4	5.1	43.0	25.2	12.1
1964	8.6	4.4	6.9	8.9	6.1	0.1	35.7	37.4	45.7	13.8	0.3	0	4.7	69.0	12.6	5.8	34.9	26.2	11.2
1965	8.6	5.1	7.2	0	7.6	3.7	24.7	29.5	32.2	11.4	0	0	4.6	66.9	0	12.4	31.4	28.2	11.8
1966	6.3	5.3	7.7	10.6	9.9	20.8	24.5	36.3	27.6	11.5	0	0	6.4	71.1	6.3	12.8	37.4	37.2	11.6
1967	7.3	6.5	10.1	13.0	19.6	20.1	25.6	33.1	27.7	10.8	0	0	7.0	67.5	5.6	8.0	29.6	38.4	16.3
1968	7.3	6.3	13.7	12.5	24.7	31.9	25.9	27.4	25.3	11.1	0	0	6.5	56.0	18.0	12.3	31.2	40.3	14.7
1969	7.3	8.9	10.8	0	14.7	40.1	23.8	39.0	21.5	9.9	0	0	0	59.3	0	18.8	8.75	42.5	0
1970	1.7	9.1	8.7	0	19.0	26.3	22.3	28.2	44.1	9.9	35.5	0	3.6	61.8	14.2	22.4	44.1	39.8	12.5
1971	1.5	9.0	10.0	12.6	11.3	48.3	26.3	25.2	29.8	0	32.5	10.3	6.4	50.2	12.3	12.5	41.3	41.8	9.8
1972	1.0	8.4	9.6	3.2	10.5	55.3	26.6	25.7	31.1	11.4	15.5	9.2	6.7	52.2	7.2	14.4	45.2	62.9	11.5
1973	1.8	14.1	13.4	15.6	21.5	47.1	26.0	27.3	30.5	0	16.1	16.3	7.7	49.4	19.3	13.6	60.0	74.0	17.9
1974	2.1	16.6	14.3	9.5	16.8	55.3	24.1	25.6	30.6	0.6	11.2	18.5	8.2	45.7	18.9	13.7	60.1	34.8	15.7
1975	1.6	14.3	13.8	9.8	14.6	58.5	26.5	23.9	35.9	1.0	12.5	27.0	8.5	46.2	22.5	12.1	61.0	36.6	13.1
1976	3.5	16.1	10.6	6.1	10.5	29.4	26.6	26.8	24.8	0.7	19.3	28.7	12.2	52.9	18.7	11.4	49.1	40.3	15.6
1977	3.8	18.9	9.6	7.3	13.5	13.7	28.1	23.2	21.9	0.4	19.9	29.5	12.2	59.7	17.4	12.2	45.6	64.1	11.3
1978	5.1	21.5	12.9	9.3	12.8	25.7	28.7	28.0	21.4	3.7	20.3	30.3	13.7	51.2	18.1	9.8	49.9	71.9	12.6
1979	6.4	24.6	10.0	10.0	12.2	16.2	24.2	31.9	20.4	0.9	20.9	33.3	11.9	50.6	19.0	7.8	39.3	74.7	12.8
1980	11.2	26.6	11.3	23.3	13.3	12.6	21.6	35.3	15.6	2.1	30.2	42.9	10.9	54.3	18.0	9.4	49.7	65.0	14.2
1981	11.0	35.7	8.3	25.8	18.9	12.5	20.3	42.0	8.9	2.4	28.6	43.2	11.5	49.0	21.5	10.1	50.0	62.9	21.3
1982	11.7	34.7	12.8	31.3	17.8	9.2	17.7	32.8	9.6	6.3	29.5	45.0	9.9	47.6	20.5	9.6	47.8	68.8	20.1
1983	12.9	31.4	9.5	29.1	14.9	11.5	18.9	39.1	9.8	6.1	32.0	49.9	10.3	43.7	22.3	8.5	51.4	18.2	19.1
1984	9.3	34.1	10.2	25.2	34.4	10.5	21.2	34.1	10.1	5.7	20.3	52.8	10.0	45.7	20.8	8.1	54.0	20.9	14.7
1985	11.9	33.3	15.3	25.2	16.8	16.8	22.9	34.2	7.8	13.7	14.2	54.3	10.3	39.3	23.1	7.4	52.6	29.5	15.1
Mean:	7.7	13.8	7.5	11.5	10.0	25.7	26.1	25.7	23.4	8.6	22.4	32.7	7.8	69.6	11.9	7.7	38.5	34.5	10.6
From:		1956		1959		1963					1963						1953	1952	1952

chus cepedianus) as the principal fisheries species. This early decline may also include the demise of the East Coast sharkhide fishery for large requiem sharks (Carcharhinidae) and other large species. The mid-1950s peak and subsequent decline may reflect declines in markets for piked dogfish and certain other small sharks.

The recent increase in U.S. catches may reflect the impact of the *JAWS* motion pictures. These Hollywood science-fiction extravaganzas heightened public interest in sharks and started a fashion for utilization of sharks as food in the United States. Cartilaginous fishes were not generally acceptable as food by the U.S. public in the decade prior to *JAWS*, although some ethnic minorities relished them. Before the *JAWS* movies, selling shark under its own name was unusual in the United States, although some shark and ray meat was sold to an unsuspecting public as "swordfish", "grayfish", and "rock scallops". After *JAWS*, shark meat suddenly became popular as a luxury food, appeared in fish markets at high prices (up to $5.00 a pound in California), and was openly served in restaurants at prices

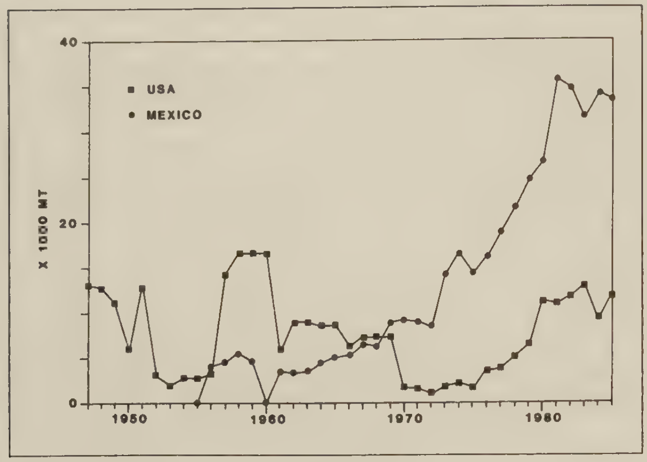

Figure 8.
Nominal catches of cartilaginous fishes from North American countries with major fisheries, including the United States and Mexico, 1947 to 1985.

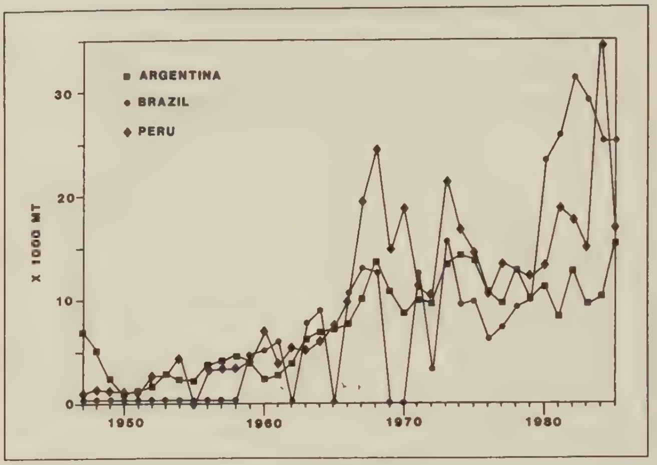

Figure 9.
Nominal catches of cartilaginous fishes from South American countries with major fisheries, including Argentina, Brazil, and Peru, 1947 to 1985.

competitive with more traditional foodfish prices. Directed fisheries arose for a number of shark species, the most important of which are the thresher shark, *Alopias vulpinus*; Pacific angelshark, *Squatina californica*; broadnose sevengill shark, *Notorynchus cepedianus*; tope shark, *Galeorhinus galeus*; and shortfin mako, *Isurus oxyrinchus*. Great white sharks, *Carcharodon carcharias*, are caught sporadically by commercial fishermen and are of high value for their meat and jaws. In addition, sports fisheries for sharks have intensified on both coasts and are particularly popular on the East Coast.

Mexico currently has about twice the chondrichthyan catch of the United States (Fig. 8) and shows a very different pattern of steady increase in catches from the early 1960s onward to a high plateau in the 1980s. Mexican catch statistics are similar to those of several other developing countries with dramatic increases in the catches of cartilaginous fishes as well as other marine organisms as these nations increasingly utilize their marine resources both for local consumption and for export to the developed world. Smoothhounds, *Mustelus* spp.; hammerheads, *Sphyrna* spp.; sharpnose sharks, *Rhizoprionodon* spp.; whitenose sharks, *Nasolamia velox*; and gray sharks, *Carcharhinus* spp. are among the most important fisheries sharks in Mexico. Large sharks are processed for hides and utilized for food.

Argentina, Brazil, and Peru are the most important chondrichthyan fishing countries in South America at present. Catch data for these countries are variable (Fig. 9) but show a broad trend (similar to that of Mexico) of dramatic changes from small-scale to major fisheries in the 1960s. "Tollos" or "cazons" (smoothhounds, *Mustelus* spp.) and "angelotes" (angelsharks, *Squatina* spp.) are among the more important fisheries sharks in the area.

Europe

Cartilaginous fish catches show divergent trends amongst the major chondrichthyan-fishing nations of Europe (Figs. 15, 16), which include France, Norway, Spain, the United Kingdom, and the U.S.S.R. Very recently (1984 and 1985) Ireland and Italy amassed cartilaginous fish catches of approximately 10,000 mt, but prior to that, these countries caught lesser amounts and were not "major" chondrichthyan-fishing nations. The United Kingdom has the closest approach to a steady-state sustainable-yield fishery (Fig. 10) amongst all major chondrichthyan-fishing countries, albeit with a trend for a gradual long-term decline. Catches rose from 27,000 mt in 1947 to a 33,000-mt maximum in 1951; they gradually declined (but with a sudden rise to 35,000 mt in 1964) to a 19,000 mt-minimum in 1982 and recovered to 24,000 mt in 1985. Norway's catches (Fig. 10) rose dramatically from 11,000 mt in 1947 to 51,000 mt in 1962, then dropped to 23,000 mt in 1969, rose again to 44,000 mt in 1970, and reached a plateau, rose yet again, and plummeted to the 1980's level of only 10,000 mt.

France shows a different pattern from those of the United Kingdom and Norway (Fig. 10), and has an irregular, large fishery with a generally increasing trend. Starting with catches of 20,000 mt in 1947, French catches dropped to about 13,000 to 15,000 mt during the 1950s but suddenly increased to a ragged plateau in the 27,000 to 39,000 mt range in the 1960s; they dropped in the early 1970s to 24,000–25,000 mt, recovered, increased, and leveled off at the 34,000–43,000 mt range in the late 1970s and early 1980s.

Spain (Fig. 11) had a steady if modest fishery in the 10,000–15,000 mt range from 1947 to the early 1970s. This declined to a few thousand mt during the 1970s and early 1980s, but it suddenly recovered to about 15,000 mt in

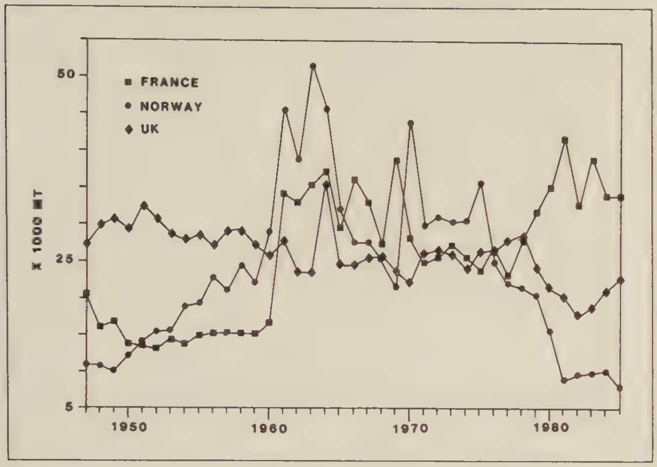

Figure 10.
Nominal catches of cartilaginous fishes from European countries with major fisheries, including France, Norway, and the United Kingdom, 1947 to 1985.

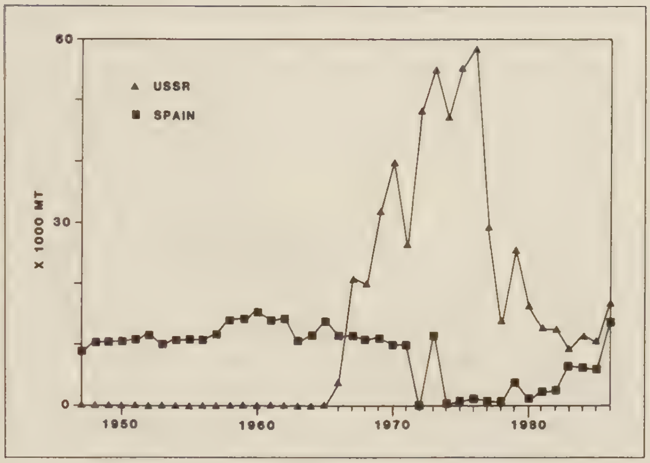

Figure 11.
Nominal catches of cartilaginous fishes from European countries with major fisheries, including the Union of Soviet Socialist Republics and Spain, 1947 to 1985.

1985. From 1947 to the early 1960s separate catch statistics for cartilaginous fishes were not available for the U.S.S.R. (Fig. 11), but probably catches were very low, less than 1,000 mt. In 1965 the U.S.S.R. reported a chondrichthyan catch of about 100 mt, but this rose to almost 4,000 mt in 1966 and then increased enormously to a peak of near 60,000 mt in 1976. With similar abruptness the Soviet catch crashed in the late 1970s and in the mid-1980s reached a level of about 9,000 to 17,000 mt, only slightly higher than Spanish catches in the same period. Piked dogfish, *Squalus acanthias*; porbeagle, *Lamna nasus*; smoothhounds, *Mustelus* spp.; tope shark, *Galeorhinus galeus*; spotted catsharks, *Scyliorhinus canicula* and *S. stellaris*; and skates, Rajidae, are prominent in European chondrichthyan catches.

Africa

Many African countries catch cartilaginous fishes, but the only one that is a known major producer at present is Nigeria (Fig. 12). Chondrichthyan catches for Nigeria were miniscule (less than 1000 mt from 1963 to 1964) or not available prior to 1971, but the catch that year, some 35,000 mt, suggests that a major fishery had been developing well before that date, perhaps in the early 1960s. The Nigerian catch declined in the mid-1970s to 11,000 mt, then rose again to a plateau of 29,000 to 33,000 mt in the late 1970s to early 1980s, but dropped again to 15,000 mt in 1985.

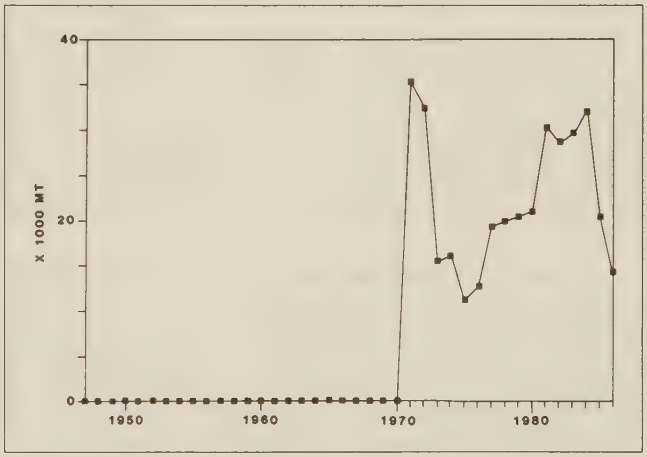

Figure 12.
Nominal catches of cartilaginous fishes from Nigeria, an African country with a major fishery, 1947 to 1985, but data available only from 1971 on.

South Africa may catch over 20,000 mt of chondrichthyans yearly, largely in the bottom trawl fishery off the Western and Southeastern Cape and in Namibian waters, but most of this catch is discarded. Chondrichthyans are largely unacceptable for human consumption when marketed as such in South Africa, and much of the populace considers them "inedible". Small local and export markets exist for some species, including fresh meat from St. Joseph (elephant fish or silver trumpeter, *Callorhinchus capensis*; fresh wings from biscuit skates, *Raja straeleni*; and dried, fresh and frozen meat from tope sharks, *Galeorhinus galeus*; cowsharks, Hexanchidae; requiem sharks, Carcharhinidae; and some other sharks. As elsewhere, shark fins are taken for the lucrative oriental sharkfin market.

Indian Subcontinent

The Indian subcontinent includes two of the most important chondrichthyan-fishing countries, India and Pakistan, which for the past twenty years have landed catches averag-

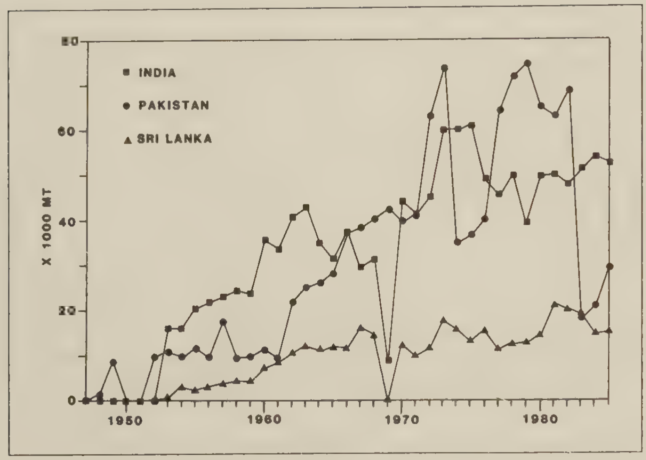

Figure 13.
Nominal catches of cartilaginous fishes from countries of the Indian Subcontinent with major fisheries, including India, Pakistan, and Sri Lanka, 1947 to 1985.

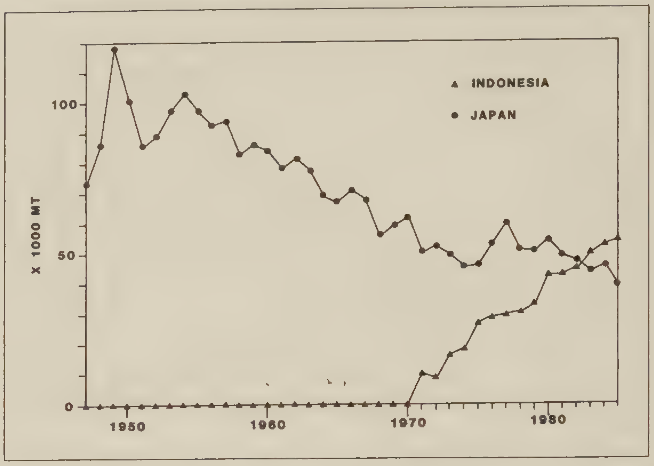

Figure 14.
Nominal catches of cartilaginous fishes from Asian countries with major fisheries, including Japan and Indonesia, 1947 to 1985.

ing over 30,000 mt per year. Sri Lanka also lands relatively large catches of cartilaginous fishes, between 10,000 to 20,000 mt in the past twenty years. A broad trend in the chondrichthyan fisheries in all three countries shows a steady increase of catches (Fig. 13), with some abrupt short-turn fluctuations and precipitous declines of uncertain cause.

Sri Lankan catches have been the most steady, with a moderate increase from the mid-1950s to the present. Indian catches steadily rose from 1952 through 1962, then began an irregular decline to a low of less than 10,000 mt in 1968, but quickly rose again to a plateau of 60,000 mt in the early 1970s and dropped again to a plateau between 40,000 to 55,000 mt from the mid-1970s to the mid-1980s. Pakistani catches have been far more erratic and have risen to a low plateau of 10,000 to 18,000 mt from 1951 to 1961. They subsequently rose steadily and steeply over the next decade to a high of about 75,000 mt in 1972. This peak was followed by an immediate twofold crash to about 35,000 mt in 1973, then by a gradual recovery to another high of about 75,000 mt in 1979. This recovery was followed by a high plateau from 1980 through 1982 at 65,000 to 70,000 mt, then by an immediate crash to 20,000 mt in 1983 with partial recovery to 30,000 mt in 1985.

All three nations have shown a plateau or slump in catches from the late 1970s to the present, and both Indian and Sri Lankan catches declined markedly in 1969. The most important fisheries sharks in the area are requiem sharks (Carcharhinidae) particularly gray sharks, *Carcharhinus* spp.; sharpnose sharks, *Rhizoprionodon* spp.; spadenose or yellow dogsharks, *Scoliodon laticaudus*; and sliteye sharks, *Loxodon macrorhinus*; but also hammerheads (Sphyrnidae) and weasel sharks (Hemigaleidae) (Compagno 1984b).

Far East

Excepting the "two Chinas," the most important chondrichthyan-fishing countries in Asia are Japan, Indonesia, Malaysia, South Korea, and Thailand. The last three countries take relatively small catches and are overshadowed by the first two. Japan has the highest sustained chondrichthyan catches known of any nation, with a mean annual catch of almost 70,000 mt from 1947 to 1985, compared with the next highest, India, with a mean annual catch of almost 39,000 mt from 1953 to 1985 (Table 5). Japanese chondrichthyan catches have shown a steady decline (Fig. 14) from their early peak of nearly 120,000 mt in 1949 to about 39,000 mt in 1985. The cause of the decline in Japanese catches, which has also been noted by Taniuchi (1990), is not obvious, but may be due in part to a shift in fisheries efforts to more valuable bony fishes, particularly scombroids. Depletion of local stocks in the western North Pacific, where most Japanese chondrichthyans are caught, is another possibility which needs investigation.

Indonesia did not report chondrichthyan catches to FAO prior to 1971, but initial catches in 1971 and 1972 were modest, in the 10,000 mt range (Fig. 14). Indonesian catches thereafter showed a steady increase to high levels and surpassed Japanese catches for the first time in 1983 when they reached nearly 50,000 mt (vs. almost 47,000 mt for Japan). Indonesian catches for 1985 continued this trend at slightly over 54,000 mt, which was the highest reported chondrichthyan catch of any single country for that year. The closest rival was India, with almost 53,000 mt for 1985, followed by Japan with about 39,000 mt.

South Korean chondrichthyan catches have fluctuated wildly in the FAO records (Fig. 15) but their general trend

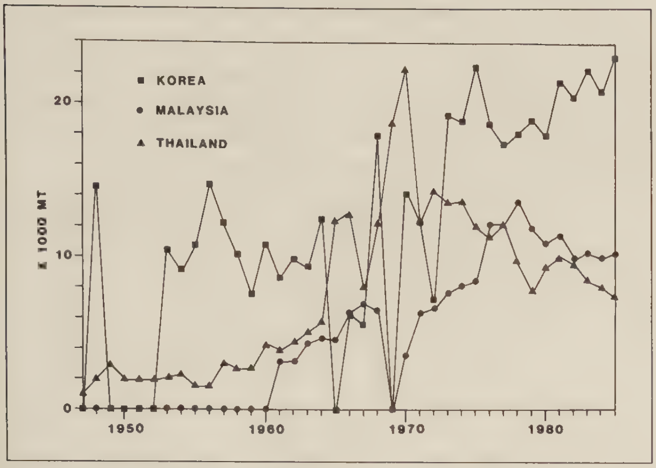

Figure 15.
Nominal catches of cartilaginous fishes from Asian countries with major fisheries, including Korea, Malaysia, and Thailand, 1947 to 1985.

has been for a broad increase, from 8,000 to 15,000 mt in the mid-1950s, to 21,000–23,000 mt in the mid-1980s. Apart from a hiatus left by the Korean War, it is not clear why Korean catch records are so variable. Korean catches were reported as zero in 1965 and 1969, but were listed as 14,000 mt in 1970; they dropped to 7,000 mt in 1971 and just as abruptly recovered to 19,000 mt in 1972.

Malaysian chondrichthyan catch data were not reported to FAO before 1960, and from this date to 1976 Malaysian catches were below 10,000 mt a year (Fig. 15). From 1976 to 1985 Malaysian catches just edged into "major" fisheries status, at about 10,000 to 14,000 mt per year. After a peak of 14,000 mt in 1978, Malaysian catches showed a slow decline and leveled off at 10,000 mt in 1985.

Chondrichthyan catch data from Thailand covers the entire period from 1947 to 1985 and may reflect the relative political stability of that country. Thai catches were minor prior to 1965 (Fig. 15) but in 1965 and 1966 rose to over 12,000 mt and, after a decline in 1967, steadily rose over the next three years to a peak of 22,000 mt in 1970. Thai catches thereafter declined steadily during the 1970s and 1980s to about 7,000 mt in 1985. The most important fisheries sharks in Thailand are inshore species, particularly requiem sharks (Carcharhinidae) but also hammerheads (Sphyrnidae); weasel sharks (Hemigaleidae); bamboo sharks, *Chiloscyllium* sp.; zebra sharks, *Stegostoma fasciatum*; and tawny sharks, *Nebrius ferrugineus*. Not included in the graphs and statistics for Asian countries is the Philippines, which prior to 1978 reported less than 10,000 mt of chondrichthyans per year, but which edged up that year with a 14,300 mt catch. Since then Philippine catches have undulated above and below the 10,000 mt mark, with 12,600 mt in 1981, 11,400 mt in 1982, 11,280 mt in 1984, and 10,900 mt in 1985.

Catches by Species of Sharks

The following section evaluates the importance of various sharks to world fisheries. The subdivision of sharks used here is by orders, following the classification of Compagno (1973, 1984a, b).

Cowsharks and Frilled Sharks (Order Hexanchiformes)

This small group is probably of minor importance to world fisheries. The frilled shark, *Chlamydoselachus anguineus* (family Chlamydoselachidae) is caught by local fishermen in small numbers in Japan. The cowsharks (family Hexanchidae) includes two large species with excellent meat for human consumption: the bluntnose sixgill shark, *Hexanchus griseus*, and the broadnose sevengill shark, *Notorynchus cepedianus*. The bluntnose sixgill shark is primarily a deep-water species that is usually caught as a bycatch of other fisheries. The broadnose sevengill shark is an inshore, temperate-water species, which is caught off California, China, Australia, and southern Africa on line gear and utilized for human consumption. The sharpnose sevengill shark, *Heptranchias perlo*, and the bigeye sixgill shark, *Hexanchus vitulus*, are small, wide-ranging, deep-water sharks of little consequence to fisheries but are caught as a bycatch in trawls and on line gear.

Dogfish Sharks (Order Squaliformes)

This is one of the most important shark groups for fisheries, but few of the 81 + species are of major importance. The bramble sharks (family Echinorhinidae) include two species of large, wide-ranging, deepwater bottom sharks of limited use to fisheries. The bramble shark, *Echinorhinus brucus*, is caught as a bycatch of bottom trawl and line fisheries in the Eastern Atlantic and is used for fishmeal and medicinal purposes, while the larger prickly shark, *Echinorhinus cookei* is seldom taken and utilized in fisheries.

The rough sharks (family Oxynotidae), are small, deep-water, bottom sharks with a wide range in the Atlantic and Western Pacific. The angular roughshark, *Oxynotus centrina*, of the Eastern Atlantic has limited use as fishmeal, liver oil, and for human consumption, but the four other species of rough sharks are unimportant to fisheries.

The dogfish sharks (family Squalidae) include over 74 species of deep-benthic, inshore, and pelagic sharks that occur in all oceans. Of these, the 9 to 12 species of spiny dogfish in the genus *Squalus* are the most important fisheries species because of their abundance and accessibility to fishing operations. The piked dogfish, *Squalus acanthias*, of inshore to deep temperate seas has traditionally supported the most intensive fisheries. These have centered in the North Atlantic and eastern North Pacific and are conducted

Table 6.

Nominal world catches of certain species of sharks, 1947–1985. Data from FAO yearbooks. Mean catches for species are calculated for entire period, except where period is delimited by "From" a year to present or "From" a year "To" a year at bottom of table. Catches for *Lamna ditropis* in period reported are for Japan only, and catches for *Galeorhinus galeus* are for Argentina only, and do not include catches from Europe, Australia, and the Eastern North Pacific. Catches in thousands of mt.

Year	*Squalus acanthias*	*Squatina* spp.	*Lamna nasus*	*Lamna ditropis*	*Mustelus* spp.	*Galeorhinus galeus*	Mixed requiem sharks
1947	17.8	?	6.1	?	7.5	?	?
1948	21.0	?	4.0	?	6.6	?	?
1949	24.1	?	3.0	?	3.5	?	?
1950	21.7	?	3.2	?	1.6	?	?
1951	28.7	?	2.4	?	1.7	?	?
1952	30.1	?	2.2	9.9	3.1	?	?
1953	28.2	?	1.8	6.4	0.3	?	?
1954	29.3	?	1.2	40.1	0.2	?	?
1955	30.9	?	1.5	5.8	2.0	?	?
1956	34.2	?	1.3	5.7	2.4	?	?
1957	33.6	?	1.7	5.1	2.8	?	?
1958	36.9	?	1.8	4.8	2.6	?	?
1959	33.3	?	1.5	4.4	3.5	?	?
1960	39.2	?	1.9	5.3	6.3	?	?
1961	37.0	?	4.3	6.7	4.1	?	?
1962	33.0	?	3.6	6.4	6.8	?	?
1963	37.0	?	6.8	5.2	7.5	?	?
1964	30.0	?	10.5	4.5	7.9	?	?
1965	28.3	?	4.9	0.1	9.7	0.8	?
1966	27.4	0.4	2.1	?	11.9	0.6	?
1967	28.6	6.5	1.6	?	18.0	0.6	?
1968	35.0	1.1	2.4	?	23.5	0.5	?
1969	36.1	1.2	2.3	?	16.0	1.0	?
1970	33.2	1.2	1.2	?	19.1	0.6	?
1971	32.8	0.8	1.3	?	16.5	0.9	?
1972	34.7	1.0	1.2	?	14.4	0.7	?
1973	43.6	0.4	0.7	?	31.9	0.4	59.9
1974	36.8	0.7	0.4	?	27.4	0.1	37.1
1975	31.1	0.4	0.7	?	25.0	0.6	36.7
1976	31.2	0.2	0.8	?	18.9	0.2	31.5
1977	28.6	0.4	0.7	?	19.9	0.01	50.4
1978	37.5	0.3	3.2	?	21.0	0.03	50.3
1979	34.8	0.1	1.6	?	16.9	0.02	50.6
1980	39.9	0.5	1.5	?	26.6	0.01	41.4
1981	36.2	0.5	1.4	?	27.5	0.03	40.3
1982	32.6	1.1	0.6	?	30.7	0.03	35.7
1983	41.0	0.3	1.1	?	31.3	0.01	28.2
1984	39.9	0.8	0.7	?	49.4	0.01	33.5
1985	41.7	0.7	0.6	?	31.7	0.01	37.3
Mean:	32.7	0.9	2.3	7.9	14.3	0.3	40.9
From:		1966		1952		1965	1972
To:		1985		1965		1985	

by the United States, Canada, the United Kingdom, Norway, France, Spain, Italy, Ireland, West Germany, and other European countries. This dogfish is fished to some extent in the Western Pacific by Japan, Korea, and New Zealand, and is regularly caught but not utilized off southern Africa. Reported world catches of piked dogfish from 1947 to 1985 (Table 6) are probably only a partial indicator of catches and catch trends, because many nations report this dogfish mixed with other *Squalus* species and with other sharks. World catches of *Squalus acanthias* (Fig. 16) as reported by FAO show a steady, if variable, increase from 18,000 mt in 1947 to almost 42,000 mt in 1985. Piked dogfish are primarily caught in bottom trawls and on line gear but are readily caught in other gear, and are utilized in various forms for human consumption and for fishmeal, liver oil, leather, and pet food.

Other species of *Squalus* dogfishes are commonly caught in the same areas as *Squalus acanthias* or in warmer waters

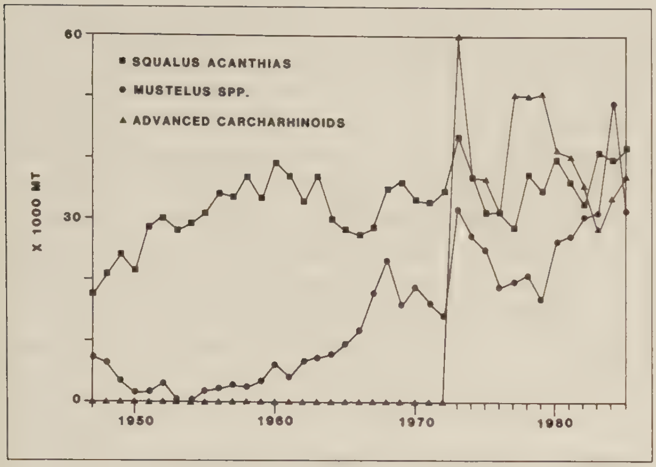

Figure 16.
Nominal world catches of certain sharks, including *Squalus acanthias*, *Mustelus* spp., and "advanced carcharhinoids" (mixed Carcharhinidae, Sphyrnidae, and Hemigaleidae), 1947 to 1985.

where it does not occur. The longnose spurdog, *Squalus blainvillei*, is caught in the temperate Eastern Atlantic and Mediterranean in gill nets, in bottom trawls, and on line gear and is utilized for human consumption. The Cuban dogfish, *Squalus cubensis*, is caught by bottom trawlers in the Gulf of Mexico for liver oil, and is sometimes used for food, while the Japanese spurdog, *Squalus japonicus*, is fished off Japan and probably elsewhere in the Western North Pacific. The shortnose spurdog, *Squalus megalops*, has a broadly discontinuous range off West and southern Africa, Australia, and the western North Pacific from Vietnam to Japan and Korea; the African and North Pacific forms have been distinguished as separate species, *S. acutipinna* and *S. brevirostris*, respectively. Shortnose dogfish can be incredibly abundant and are mostly taken by bottom trawls and utilized for human consumption. The shortspine spurdog, *Squalus mitsukurii*, is common in the western North Pacific and is caught in fisheries off Japan. Similar and possibly identical shortspine dogfishes have a wide range in temperate and tropical waters and recently were discovered in commercial quantities in deep water off the west and southeast coasts of South Africa.

The giant Greenland shark, *Somniosus microcephalus*, has long been fished off Greenland, Norway, and Iceland for liver oil and as food, but catch figures are not available and catches probably are small; the similar Pacific sleeper shark, *S. pacificus*, does not support a fishery. Several species of deepwater benthic dogfish, particularly members of the genera *Centrophorus*, *Centroscymnus*, *Dalatias*, *Deania*, and *Scymnodon*, have huge livers that are full of squalene-rich liver oil, and these have been fished for their livers in the Western North Pacific. The refined squalene is used for medicinal purposes and cosmetics in Japan and elsewhere. Deep-water dogfishes are sometimes targeted for human consumption, but many bottom-dwelling species are probably caught as a bycatch of offshore bottom trawl fisheries directed at benthic teleosts and are processed for fishmeal.

Sawsharks (Order Pristiophoriformes, Family Pristiophoridae)

This group includes five species of small, flat-headed, bottom sharks of the Western Pacific, southern Africa, and the Bahamas. Only the longnose sawshark, *Pristiophorus cirratus*, and shortnose sawshark, *P. nudipinnis*, of southern Australia are apparently sufficiently abundant to support a directed fishery. Australian sawsharks are caught by bottom trawl and line gear and utilized fresh for human consumption.

Angelsharks (Order Squatiniformes, Family Squatinidae)

There are at least thirteen species of angelsharks (genus *Squatina*), which occur in temperate and subtropical continental waters in most oceans. Angelsharks are flat-bodied bottom-dwellers which are readily caught by bottom trawlers and yield excellent meat for human consumption. Angel sharks are also utilized for fishmeal, liver oil, leather, and shagreen for woodworking. Several species are fished in limited or considerable quantities worldwide: the sawback angelshark, *Squatina aculeata*, off West Africa; the Argentine angelshark, *S. argentina*, off Argentina; the Pacific angelshark, *S. californica*, off California, in the Gulf of California, and off Peru and Chile; the Japanese angelshark, *S. japonica*, and clouded angelshark, *S. nebulosa*, off China, Taiwan, Japan, and Korea; the smoothback angelshark, *S. oculata*, off West Africa and in the Mediterranean Sea; and the European angelshark, *S. squatina*, in the North Atlantic and Mediterranean. Angelshark catches reported by FAO (Table 6) are small, from 100 to 6500 mt yearly from 1966 to 1985; this probably represents only a fraction of the actual catch, mostly from South America and Europe. Trends for these catches are difficult to interpret. Richards (1987) has documented the high-value directed fishery for Pacific angelsharks in California, which developed there after the *JAWS* motion pictures aroused public interest in shark meat.

Bullhead Sharks (Order Heterodontiformes, Family Heterodontidae)

The eight species of bullhead sharks (genus *Heterodontus*) are warm-temperate to tropical, inshore sharks of the Indian and Pacific Oceans. None are abundant enough to be important in fisheries, although some are eaten or made into fishmeal. Divers catch the horn shark, *Heterodontus francisci*, by hand in California and make jewelry of its heavy dorsal fin spines.

Carpet Sharks (Order Orectolobiformes)

The seven families and at least 32 species of carpet sharks are mostly warm-temperate and tropical, inshore, bottom sharks with greatest diversity in the Western Pacific, particularly in Australian waters. As a group they are of limited interest to fisheries compared to other tropical sharks but are noteworthy for their thick and often attractively patterned skins, which make excellent leather. Fins of the larger species are used in the oriental sharkfin trade.

The collared carpet sharks (family Parascylliidae) include eight species of small sharks of the Western Pacific that are incidental catches of bottom trawlers and bottom longliners and probably are of little use to fisheries. The blind sharks (family Brachaeluridae) include two small Australian inshore sharks, one of which is commonly caught by sports anglers on rod and reel and by bottom trawlers but is probably not utilized to any great extent. The wobbegong sharks (family Orectolobidae) include at least six species of large, flat-bodied benthic sharks in the Western Pacific. Several species are used for food and occasionally for leather, but they are probably only a minor component of shark fisheries where they occur. Wobbegongs are taken in bottom trawls, in gill and trammel nets, in lobster pots and traps, by spear, and with line gear, and are also caught by sports anglers.

The longtailed carpet sharks (family Hemiscylliidae) include 12 species of small inshore sharks of the tropical Indian Ocean and Western Pacific. The epaulette sharks, *Hemiscyllium* spp., are unimportant for fisheries but the bamboo sharks, *Chiloscyllium* spp., are commonly fished where they occur, including Madagascar, India, Pakistan, Sri Lanka, Thailand, and elsewhere, and are utilized for human consumption. Because of their small size and moderate abundance, bamboo sharks are probably less important for tropical fisheries than small inshore requiem sharks (Carcharhinidae) where both occur together. Zebra sharks, *Stegostoma fasciatum* (family Stegostomatidae), are large bottom sharks of the Indo-West Pacific that are regularly caught in bottom trawls, in gill nets, and on line gear off Pakistan, India, Thailand, Malaysia, Taiwan, and elsewhere. Zebra sharks are utilized for human consumption, for vitamin oil (derived from their livers), for their fins, and for fishmeal, but are of limited importance to fisheries.

The nurse sharks (family Ginglymostomatidae) include three species of tropical, inshore, benthic sharks which are fished where they occur, but are probably less important than requiem sharks (Carcharhinidae) in places where both are found together. The nurse shark, *Ginglymostoma cirratum*, of the tropical Atlantic and Eastern Pacific is commonly caught with bottom trawls, gill nets, and line gear and is eaten and processed for its vitamin-rich liver oil, fish meal and leather. The tawny shark, *Nebrius ferrugineus* (also termed *N. concolor*), of the Indo-Pacific is caught for its meat, for its liver oil, for fishmeal, and for its fins in Pakistan, India, Thailand, and probably elsewhere. Large individuals are prized by sports anglers in Australia because of their vigorous fight. The shorttailed nurse shark, *Pseudoginglymostoma brevicaudatum*, is caught by artisanal fishermen off East Africa.

The whale shark, *Rhincodon typus* (Family Rhincodontidae), is found in all temperate and tropical seas. This giant filter-feeder is or has been the subject of small net and harpoon fisheries off Senegal, India, Pakistan, Taiwan, and possibly China, and is mostly utilized for its flesh, but catches are probably small.

Mackerel Sharks (Order Lamniformes)

The seven families and 15 species of this group are mostly large, wide-ranging sharks, many of which are targeted for fisheries. The rare, deep-water goblin shark, *Mitsukurina owstoni* (family Mitsukurinidae), is only occasionally taken on line gear, in deep bottom trawls, deep-set gill nets, and other gear, and has been utilized for human consumption and possibly for fishmeal. The small crocodile shark, *Pseudocarcharias kamoharai* (family Pseudocarchariidae), is a circumtropical oceanic species that is commonly caught on tuna longlines, but at least in Japan was considered unsuitable for human consumption. Its large liver is potentially valuable for squalene. The megamouth shark, *Megachasma pelagios* (family Megachasmidae), is a rare, large, filter-feeding shark of the Pacific and Indian Oceans with no fisheries value.

The sand tiger sharks (family Odontaspididae) include one species that is generally fished wherever it occurs, the sand tiger shark, *Carcharias taurus* (formerly *Eugomphodus* or *Odontaspis taurus*; also termed spotted raggedtooth shark or gray nurse shark). This large, common, inshore shark is found along most continental coasts except the Eastern Pacific, and is caught on line gear, gill nets, and in trawls for its meat, fishmeal, vitamin-rich liver oil, fins, and hides. It is often caught by sports anglers and was formerly shot by spearfishing divers for sport in Australia and to a lesser extent South Africa. The smalltooth sand tiger shark, *Odontaspis ferox*, is a deep-water shark with a wide and spotty circumtemperate and tropical range, but is fished only in small numbers in the Eastern Atlantic and western North Pacific for its meat, for the squalene oil in its liver, and possibly for its fins. The deep-water bigeye sandtiger, *Odontaspis noronhai*, has a very spotty range in the Atlantic, Central Pacific, and possibly western Indian Ocean. It has been taken with deepset line gear by commercial fishermen but is not utilized.

The giant filter-feeding basking shark, *Cetorhinus maximus* (family Cetorhinidae), has been the subject of sporadic, directed, local fisheries that are usually worked by small boats using harpoons, in the North Atlantic, Eastern Pacific, and western North Pacific. Such fisheries quickly collapse when the limited stocks of basking sharks are overfished, and stocks may take a decade or more to recover from intensive fishing pressure. Basking sharks are also accidentally caught in gill nets and trawls, and have been occasionally persecuted as pests in the eastern North Pacific because they wreck salmon gill nets.

Thresher sharks (family Alopiidae, genus *Alopias*) are large, coastal and oceanic, wide-ranging sharks that yield some of the finest shark meat, which is marketed fresh, smoked, or dried for human consumption. The livers of threshers yield vitamin oil, while their fins are used for sharkfin soup base and their hides for leather. Commercial fishermen usually catch threshers on longlines but also catch them in gill nets and trawls. Sports anglers prize threshers and catch them on rod and reel, often after a strong fight. All three species are fished, probably throughout their extensive ranges, but possibly the most important species is the thresher shark or common thresher, *Alopias vulpinus*. The rise and apparent decline of the thresher gillnet fishery off California is documented by Bedford (1987). The bigeye thresher, *A. superciliosus*, has been intensively fished in the western North Atlantic, Central Pacific, and western Indian Ocean; fisheries for the small pelagic thresher, *A. pelagicus*, are centered in the Northwestern Indian Ocean, western North Pacific, and Central Pacific.

The five species of mackerel sharks (family Lamnidae) are large to gigantic, wide-ranging, coastal, and oceanic species that are important fisheries catches worldwide. They are caught mostly by line gear and gill nets but also in trawls, with harpoons, and even in trap nets. The meat of some of these sharks is of high quality for human consumption and is equivalent to that from threshers. Additionally, they are utilized for their vitamin-rich liver-oil, fins, hides, fishmeal, jaws, and teeth. Sports anglers prize some of the species, particularly shortfin makos, great white sharks, and porbeagles, as game sharks and for food.

One of the most important fisheries species is the porbeagle, *Lamna nasus*, which has a wide range in the Atlantic, Indian Ocean, and South Pacific. The commercial porbeagle fishery in European seas is relatively well-documented and represented in the FAO yearbooks from 1947 to 1985 (Table 6), but southern hemisphere catches of this shark, which are probably considerable, are less well known. Porbeagle catches in the North Atlantic show a drop after a 1947 catch of 6,000 mt to a low of about 2,000 mt in the 1950s, then a sudden increase to a peak catch of almost 11,000 mt in 1964 (reflecting the intensive Norwegian longline fishery for them), then a crash in stocks and low catch levels mostly below 2,000 mt to the present. The salmon shark, *Lamna ditropis*, of the north Pacific has been fished by Japan for a long time, and has recently generated much interest as a fisheries target for U.S. commercial fishermen in Alaska (Paust and Smith 1986). Catch trends for this species are less well known than for the porbeagle in the North Atlantic. The FAO yearbooks published Japanese catch statistics of this species from 1952 to 1965 (Table 6); if the gigantic catch of 1954 is not a data error, the pattern is similar to that of the North Atlantic porbeagle.

Fisheries catches of the shortfin mako, *Isurus oxyrinchus*, and longfin mako, *I. paucus*, must be considerable throughout their ranges, yet little is known of these on a worldwide basis. To some sports anglers, the shortfin mako is an ultimate big game fish, to be ranked with sailfish or marlin for the energetic, leaping battle it often offers. Shortfin mako are fished in the Mediterranean, West Africa, off Cuba and the Atlantic Seaboard, in the Gulf of Mexico and Caribbean, off southern California, the West-Central Pacific, and the tropical Indian Ocean. Longfin mako are taken in the Western Atlantic and the western Central Pacific, and probably elsewhere where they occur.

The great white shark, *Carcharodon carcharias*, is apparently nowhere abundant enough to support a significant fishery, and prior to the *JAWS* movies was mostly taken as a sporadic bycatch of other fisheries with a wide variety of gear and was often discarded. A very small number of sports anglers, mostly in Australia and South Africa, have practiced "monster-fishing" for white sharks with heavy gear. In the post-*JAWS* period, white sharks were sought by commercial fishermen for their meat in some places (i.e., California), but these sharks were also increasingly caught by sports anglers, shot by divers, captured alive for large public aquaria, captured and displayed as frozen or preserved cadavers, and, most disturbingly, caught only for their jaws. Properly prepared, the jaws of large white sharks in the 4- to 5-m range have been sold for $2,000 to $5,000 each in the United States, and this market has encouraged erratic spot fisheries in California, New York, South Africa, South Australia, and possibly elsewhere. One fisherman in South Africa recently (1987) caught 18 large white sharks off the Western Cape and extracted their jaws for the U.S. market; their carcasses were discarded at sea.

Ground Sharks (Order Carcharhiniformes)

This large order includes eight families and over 207 species and is the dominant group of sharks in the world's oceans. Two of the families, the houndsharks (Triakidae) and requiem sharks (Carcharhinidae), are among the most important fisheries sharks. The catsharks (family Scyliorhinidae) are the largest family of sharks, with over 101 species, but few are of significance to fisheries. Some of the deep-water forms are probably a miniscule component of fishmeal produced by international offshore bottom-trawlers. The most important fisheries species are two European members of the genus *Scyliorhinus*, the small-spotted catshark, *S. canicula*, and the nursehound or large-spotted catshark, *S. stellaris*, both of which are eaten and made into fishmeal. In southern African waters, members of the genera *Poroderma*, *Haploblepharus*, *Halaelurus*, *Holohalaelurus*, *Galeus*, and *Scyliorhinus* are often taken by sports anglers and trawlers but are returned to the water alive or discarded.

The finback catsharks (family Proscylliidae) are a small group of six species of primarily deep-water sharks that have little importance to fisheries; one species, the graceful catshark, *Proscyllium habereri*, is caught by Taiwanese trawlers and is probably used for human consumption. The large, rare, deep-water, false catshark, *Pseudotriakis microdon* (family Pseudotriakidae), has a wide range in most seas but is of no importance to fisheries. The small, inshore, barbeled houndshark, *Leptocharias smithii* (family Leptochariidae), of the tropical Eastern Atlantic is sufficiently common to be caught as a bycatch of trawl, line, and gill net fisheries in various African countries, where it is utilized for human food and for leather, but it is not a major fisheries species.

The houndshark (family Triakidae), a large, temperate and tropical family of over 34 species of small to moderate-sized sharks, are of major importance for commercial shark fisheries in temperate waters and also for sports anglers who catch them in considerable quantities. The tope shark, *Galeorhinus galeus* (also known as soupfin shark, school shark, vaalhaai, vitamin shark, and oil shark), of temperate waters has generally been an important fisheries species, and is utilized for food, for its high-potency vitamin oil, and for its fins. Significant fisheries for tope sharks have existed in European waters and off southern Africa, Uruguay and Argentina, California, Australia, and New Zealand, but have collapsed or decreased owing to overfishing or to concern about high levels of mercury in their flesh. The whiskery shark, *Furgaleus macki*, of southwestern Australia has supported a considerable food fishery off western Australia. The Japanese topeshark, *Hemitriakis japanica*, is commonly caught off Japan, Korea, Taiwan, and probably China. The flapnose houndshark, *Scylliogaleus quecketti*, of South Africa is mostly caught by shore anglers but is not used to any extent. The deep-water blackfin tope, *Hypogaleus hyugaensis*, of southern Africa and Japan is caught by trawlers and with line gear and gill nets, and is of little commercial importance. This is also true of the bigeye houndsharks, *Iago* spp., in the Indo-West Pacific and of the rare New Guinean sailfin houndshark, *Gogolia filewoodi*.

The genus *Triakis* includes four species of common inshore houndsharks that are often caught by sports anglers and commercial fishermen. The spotted houndshark, *T. maculata*, of Peru, Chile, and the Galapagos is fished commercially for human consumption. The sharptooth houndshark or spotted gully shark, *T. megalopterus*, of southern Africa is mostly caught by sports anglers and is largely discarded. The banded houndshark or dochizame, *T. scyllium*, of the western North Pacific is fished commercially off Japan and probably Korea and China. The leopard shark, *T. semifasciata*, of the eastern North Pacific is caught by sports anglers, divers, and small-scale commercial fishermen for human consumption.

Currently the most important houndsharks for commercial and sports fisheries are the 20 + species of smoothhounds or gummy sharks, *Mustelus* spp., of most temperate and tropical continental seas. These invertebrate-feeding, abundant, mostly inshore sharks are readily caught by local fisheries using line gear, gill nets, trap nets, and trawls. Smoothhounds are mostly utilized for food but also for their vitamin-rich liver oil and for fish meal. *Mustelus* spp., locally referred to as "tollos" or "cazons," have long been an important catch in Latin America. Catches for *Mustelus* spp., reported in aggregate (Table 6) have steadily increased from 1947 to 1985, with a peak catch near 50,000 mt in 1984. All the species are fished, but the most important fisheries species include the gummy shark, *Mustelus antarcticus*, of temperate Australian seas; the starry smoothhound, *M. asterias*, of Europe and North Africa; the gray smoothhound, *M. californicus*, brown smoothhound, *M. henlei*, and sicklefin smoothhound, *M. lunulatus*, of the Eastern Pacific; the dusky smoothhound, *M. canis*, of the Western Atlantic; the spotless smoothhound, *M. griseus*, and starspotted smoothhound, *M. manazo*, of the Western Pacific (the latter also off East Africa); the spotted estuary smoothhound or rig, *M. lenticulatus* of New Zealand; the speckled smoothhound, *M. mento*, and narrownose smoothhound, *M. schmitti*, of South America; the Arabian smoothhound, *M. mosis*, of the western Indian Ocean and Red Sea; and the smoothhound, *M. mustelus*, of the Eastern Atlantic and southwestern Indian Ocean.

The weasel sharks (family Hemigaleidae) include six species of small to medium-sized, inshore sharks of the warm-temperate and tropical Eastern Atlantic and Indo-West Pacific. Five species of these sharks are regularly caught by line gear, gill nets, and bottom trawls, and utilized mostly for human consumption. The Atlantic weasel shark, *Paragaleus pectoralis*, is regularly caught off West Africa. The straighttooth weasel shark, *P. tengi*, is a minor component of fisheries catches off Taiwan and China. Three species that are regularly fished in the Indo-West Pacific and which can be locally abundant include the hooktooth shark, *Chaenogaleus macrostoma*; the snaggletooth shark, *Hemipristis elongatus*; and the sicklefin weasel shark, *Hemigaleus microstoma*. The meat of the snaggletooth shark is especially prized in India.

The large family of requiem sharks (family Carcharhinidae) has at least 50 species in all tropical and temperate seas. This is the most important family of fisheries sharks in warm seas and the open oceans. Many of the species are large and of value for their meat and fins, but also for their vitamin-rich liver oil, for hides, and for fishmeal. Several of the small inshore species are amongst the most abundant small sharks where they occur, and seem to take the place of *Squalus* dogfish (family Squalidae) in shallow tropical waters. Several species are regularly caught by sports anglers and some are big game species. Requiem sharks are caught with line gear, gill nets, trawls, trap nets and other gear. Partial FAO statistics exist for mixed "advanced carcharhinoids" (Table 6), which probably include requiem sharks, weasel sharks and hammerheads. Recorded catches from 1971 to 1985 are high, between 30,000 and 60,000 mt, with a possible decline in recent times (Fig. 16).

Almost all of the 30 species of gray sharks, *Carcharhinus* spp., are fisheries sharks, with the possible exception of a few poorly known, rare species. The most important coastal and semioceanic species include the Western Atlantic blacknose shark, *Carcharhinus acronotus*; the Indo-Pacific silvertip shark, *C. albimarginatus*; the deep-water bignose shark, *C. altimus*; the copper shark or bronze whaler, *C. brachyurus*; the spinner shark, *C. brevipinna*; the closely related Indo-West Pacific whitecheek and blackspot sharks, *C. dussumieri* and *C. sealei*; the bull shark, *C. leucas*; and possibly the closely similar pigeye or Java shark, *C. amboinensis*; the blacktip shark, *C. limbatus*; the Indo-Pacific hardnose shark, *C. macloti*, and blacktip reef shark, *C. melanopterus*; the dusky shark, *C. obscurus*; the Caribbean reef shark, *C. perezi*; the sandbar shark, *C. plumbeus*; the smalltail shark, *C. porosus*, of American waters; the Atlantic night shark, *C. signatus*; the spottail shark, *C. sorrah*; the Indo-West Pacific blacktail reef shark, *C. wheeleri*; and the gray reef shark, *C. amblyrhynchos*. The oceanic whitetip shark, *C. longimanus*, silky shark, *C. falciformis*, and blue shark, *Prionace glauca*, are the commonest sharks in warm-temperate and tropical oceanic waters, and are frequently caught on pelagic longlines and gill nets and in tuna purse seines.

The tiger shark, *Galeocerdo cuvieri*, the largest requiem shark, is a common fisheries catch; large individuals are prized by big game sports anglers. The Indo-Pacific river sharks, *Glyphis* spp., are poorly known, but probably are utilized where they are caught. The daggernose shark, *Isogomphodon oxyrhynchus*, of the tropical Western Atlantic is taken in small numbers in inshore waters by local fishermen, as is the Indo-West Pacific broadfin shark, *Lamiopsis temmincki*, in India. The small, wide-ranging sliteye shark, *Loxodon macrorhinus*, of the Indo-West Pacific is an important fisheries species in southeastern India. The whitenose shark, *Nasolamia velox*, of the tropical Eastern Pacific is commonly caught in the Gulf of California. The two large, inshore lemon sharks, *Negaprion acutidens* and *N. brevirostris*, are regularly fished wherever they occur. The small sharpnose sharks, *Rhizoprionodon* spp., of inshore, warm-temperate and tropical seas are often extremely abundant and important for fisheries. Prominent fisheries species include the milk shark, *R. acutus*, of the tropical Eastern Atlantic and Indo-West Pacific; the Brazilian sharpnose shark, *R. lalandei*, of the Southwestern Atlantic; the Pacific sharpnose shark, *R. longurio*, of the Eastern Pacific; the Indo-West Pacific gray sharpnose shark, *R. oligolinx*; and Caribbean sharpnose shark, *R. porosus*, of South America and the Caribbean. A similar, abundant fisheries species is the spadenose shark, *Scoliodon laticaudus*, of the Indo-West Pacific, of particular importance in Indian and Pakistani waters. The whitetip reef shark, *Triaenodon obesus*, is fished throughout its broad Indo-Pacific range and is one of the commonest sharks on coral reefs.

The eight species of hammerhead sharks (family Sphyrnidae) are wide-ranging, warm-temperate and tropical sharks, all of which are probably caught in fisheries. They are utilized for their meat, their liver oil (which has high levels of vitamin A), for their fins, and for fishmeal, and are caught on line gear, in gill nets, in trawls, and with other gear. The most wide-ranging, abundant, and important fisheries species are the large scalloped hammerhead, *S. lewini*, and smooth hammerhead, *S. zygaena*, which complement each other in tropical and warm temperate waters. The great hammerhead, *S. mokarran*, the largest species in the family, is less abundant than the scalloped and smooth hammerheads but is widely fished along with them. Of the smaller species, the Indo-West Pacific winghead, *Eusphyra blochii*, bonnethead, *Sphyrna tiburo*, and scoophead, *S. media*, of the Eastern Pacific and Western Atlantic; and the smalleye hammerhead, *S. tudes*, of the tropical Western Atlantic can be locally abundant and are commonly fished. The uncommon scalloped bonnethead, *S. corona*, of the Eastern Pacific is probably a minor fisheries catch compared to other hammerheads.

Relative Importance of Shark Species to Fisheries

An attempt was made to grade the 360 + living species of sharks into four qualitative categories of importance to contemporary fisheries (Table 7). The *minimal* category includes rare and unusual (or uncommon) species of sharks that are not known from fisheries or that are occasionally taken in fishing operations. Examples of minimal-catch species include many of the deep-water catsharks (Scyliorhinidae), many small, deep-benthic and oceanic dogfish (Squalidae), the frilled shark, *Chlamydoselachus anguineus*, the megamouth shark, *Megachasma pelagios*, most bullhead sharks, (Heterodontidae), and many others.

The *minor* category includes species that are regularly caught in small numbers and used but that are not important because of limited value and numbers. Examples of minor-catch species include many dogfish sharks (Squalidae), angelsharks (Squatinidae), many carpet sharks (Orectolobiformes), and some lamnoids (certain odontaspidids as well as mitsukurinids and pseudocarchariids). The *moderate* category includes species that are regularly caught in substantial amounts or are caught in small numbers but are disproportionally valuable because of products made from them. Moderate-catch species include the broadnose

Table 7.

Shark species, families, and orders ranked in relative importance to fisheries. For detailed explanation, see text.

	Fishery ranking								
	Minimal		Minor		Moderate		Major		
Species	No.	%	No.	%	No.	%	No.	%	Total spp.
Hexanchiformes		40		20	2	40	—	—	5
Chlamydoselachidae	1	100	—	—	—	—	—	—	1
Hexanchidae	1	25	1	25	2	50	—	—	4
% Total sharks:		0.5		0.3		0.5		—	
Squaliformes	53	65	23	28	4	5	1	1	81
Echinorhinidae	1	50	1	50	0	0	0	0	2
Squalidae	48	65	21	28	4	5	1	1	74
Oxynotidae	4	80	1	20	—	—	—	—	5
% Total sharks:		14		6		1		0.3	
Pristiophoriformes	1	20	2	40	2	40	—	—	5
Pristiophoridae	1	20	2	40	2	40	—	—	5
% Total sharks:		0.3		0.5		0.5		—	
Squatiniformes	6	46	4	31	3	23	—	—	13
Squatinidae	6	46	4	31	3	23	—	—	13
% Total sharks:		2		1		0.8		—	
Heterodontiformes	6	75	2	25	—	—	—	—	8
Heterodontidae	6	75	2	25	—	—	—	—	8
% Total sharks:		2		0.5		—		—	
Orectolobiformes	15	47	10	31	7	22	—	—	32
Parascylliidae	5	71	2	29	—	—	—	—	7
Brachaeluridae	1	50	1	50	—	—	—	—	2
Orectolobidae	3	50	3	50	—	—	—	—	6
Hemiscylliidae	6	50	3	25	3	25	—	—	12
Stegostomatidae	—	—	—	—	1	100	—	—	1
Ginglymostomatidae	—	—	1	33	2	67	—	—	3
Rhincodontidae	—	—	—	—	1	100	—	—	1
% Total sharks:		4		3		2		—	
Lamniformes	2	13	3	20	6	40	4	27	15
Odontaspididae	1	33	1	33	1	33	—	—	3
Mitsukurinidae	—	—	1	100	—	—	—	—	1
Pseudocarchariidae	—	—	1	100	—	—	—	—	1
Megachasmidae	1	100	—	—	—	—	—	—	1
Cetorhinidae	—	—	—	—	1	100	—	—	1
Alopiidae	—	—	—	—	2	67	1	33	3
Lamnidae	—	—	—	—	2	40	3	60	5
% Total sharks:		0.5		0.8		2		1	
Carcharhiniformes	111	54	21	10	51	25	24	12	207
Scyliorhinidae	97	96	2	2	2	2	—	—	101
Proscylliidae	5	83	1	17	—	—	—	—	6
Pseudotriakidae	1	100	—	—	—	—	—	—	1
Leptochariidae	—	—	—	—	1	100	—	—	1
Triakidae	4	12	9	26	12	35	9	26	34
Hemigaleidae	1	17	—	—	5	83	—	—	6
Carcharhinidae	3	6	5	10	29	58	13	26	50
Sphyrnidae	—	—	4	50	2	25	2	25	8
% Total sharks:		30		6		14		7	
Grand totals:	196	54	66	18	75	20	29	8	366

sevengill shark and possibly the bluntnose sixgill shark; some species of *Squalus* dogfishes, the Australian longnose and shortnose saw sharks; at least three species of angelsharks, *Squatina* spp.; certain carpet sharks (Orectolobiformes), including some bamboo sharks, *Chiloscyllium* spp., and the large species of *Nebrius*, *Ginglymostoma*, *Stegostoma*, and *Rhincodon*; several lamnoids, including the sand tiger, *Carcharias taurus*, basking shark, the bigeye and pelagic threshers, possibly the longfin mako, and the great white shark; and numerous ground sharks (Carcharhiniformes) including the two European spotted catsharks, *Scyliorhinus*, the barbeled houndshark, and several species of houndsharks, weasel sharks, requiem sharks, and hammerheads.

The *major* category includes important fisheries species that are caught in large amounts or are caught in lesser numbers but are of high value. Examples of major-catch species include the piked dogfish, *Squalus acanthias*; some lamnoids, including thresher sharks, *Alopias vulpinus*, porbeagle sharks, salmon sharks and shortfin makos; certain houndsharks (tope shark and several species of *Mustelus*); several species of large, abundant, wide-ranging requiem sharks (Carcharhinidae) that are fished wherever they occur; and at least two common, wide-ranging hammerheads (scalloped and smooth hammerheads).

In Table 7, the shark orders and families with numbers of species are listed and ranked in each of the four categories of relative importance to fisheries. For each category, the number of species in it is listed as a percentage of total species in the family, as a percentage of total species in the order, and as a percent of total species of sharks. In the absence of quantitative data on catches of every species, this presentation is somewhat preliminary and arbitrary but may be workable as a temporary expedient. By this scheme, approximately 8% of the shark species are major, 20% moderate, 18% minor, and 54% minimal fisheries species.

Shark Fisheries and Conservation

Holden (1973, 1974, 1977) raised doubts on the possibility of sustaining high-level fisheries for sharks and other elasmobranchs. Because chimaeras have similar reproductive strategies to those of elasmobranchs, these doubts can be readily extended to all chondrichthyans. Using case histories for local shark fisheries available at the time, including the tope shark, *Galeorhinus galeus*, off California (Ripley 1946) and Australia (Olsen 1954); the basking shark, *Cetorhinus maximus*, fishery off the United Kingdom (Parker and Stott 1965); and U.K.-Norwegian fisheries for piked dogfish, *Squalus acanthias* (Holden 1968). Holden suggested that initial exploitation of sharks results in rapid decline in catch rates and, in some cases, a complete collapse of the fishery. All known elasmobranchs and holocephalians have relatively slow growth rates and low reproductive potential. Elasmobranchs were considered by Holden (1973, 1974, 1977) to be limited by their modes of reproduction, which are geared to producing limited numbers of large cased eggs or young. Their minimum age at maturity and their fecundity apparently have narrow ranges and limits that allow little flexibility in compensating for increased exploitation. Classical models of fisheries management, based on oviparous teleosts with high fecundity, assume that the recruitment rate is virtually independent of stock size. These models were shown by Holden (1974, 1977) to be irrelevant for elasmobranchs (and chondrichthyans), because stock size and recruitment are closely related, and reduction of stocks causes reduction of recruitment. Holden (1973, 1974, 1977) noted that the several species of skates (Rajidae) fished in the Eastern North Atlantic are more fecund than most sharks (oviparous, with 50–100 eggs per female per annum), and resist fishing pressure better than livebearing fisheries sharks in the area (eg., porbeagle and piked dogfish), but even catches of these have declined after sustained fishing pressure. Most sharks that figure in moderate and major fisheries (as defined above) are livebearers and are probably more vulnerable to fisheries pressure than skates fished in the Eastern Atlantic. Little is known of the reproductive biology of most oviparous sharks that occur in fisheries, except the European spotted catsharks, *Scyliorhinus canicula* and *S. stellaris*, which may be less fecund than inshore skates.

From research on the piked dogfish, *Squalus acanthias*, fishery off Norway and the United Kingdom, Holden (1968, 1974) suggested that adult females had to be given considerable protection if sustainable fisheries were to be maintained. This was impossible with the methods used by local bottom trawl and longline fisheries to catch these sharks, which are a bycatch of the trawl fishery. Holden (1968, 1974) suggested that the numbers of reproductive females in unexploited piked dogfish populations were optimal for the replacement of losses due to natural mortality. Although there was a slight increase in fecundity in exploited dogfish stocks off the United Kingdom and Norway in comparison to unexploited stocks in the Western Atlantic, this increase was calculated by Holden to be insufficient to compensate for fisheries pressure, and Eastern Atlantic stocks of piked dogfish would (and did) decline accordingly. Holden (1973, 1974) concluded that elasmobranch stocks offer very limited opportunities for long-term exploitation, but that they were worth exploiting because of their value to commercial fisheries.

How do Holden's (1973, 1974) conclusions on the limits of elasmobranch fisheries apply to the FAO fishery data analyzed above, which show a threefold increase in the world chondrichthyan catch in the past forty years? Despite the lack of detailed data for most species, Holden's conclusions are apparently not contradicted for world and local fisheries catches. The catch data suggest, however, that sharks, rays, and chimaeras were underexploited in many areas forty years ago. The general pattern of fisheries exploitation of cartilaginous fishes since 1947 shows an increase and sometimes a decline of well-established, local bycatch and directed fisheries in certain areas such as the eastern North Atlantic and western North Pacific. This trend in established fisheries is coupled with the gradual or sudden rise, and sometime precipitous decline, of more recent major chondrichthyan fisheries elsewhere, which were probably tapping previously underexploited stocks. These recently established fisheries include at least three types: 1) local, mostly bycatch fisheries of numerous developing countries (e.g., Mexico, India, Pakistan, and Indonesia); 2) Wide-ranging offshore bycatch and directed fisheries of several developed countries that have invested in long-range international fishing fleets (e.g., U.S.S.R., Japan, South Korea, and Taiwan); 3) Local directed fisheries of developed countries in which consumption of sharks has suddenly become fashionable (e.g., the United States).

Some of these national fisheries catches, as noted above, are already declining, although the world catch curve is still rising with a possible slight flattening trend and at a lower rate than that of the three major bony fish groups (clupeoids, scombroids, and gadoids). World fisheries will eventually run out of underexploited or unexploited chondrichthyan populations in accessible areas, and the catch curve probably will flatten out still further and even decline in the next few decades as more chondrichthyan populations become overexploited and accordingly decline.

The long-range prospect for cartilaginous fishes in the next century seems grim. Their reproductive biology is ultimately unable to cope with increasing fisheries pressures by ever-burgeoning human populations, particularly in developing maritime nations or inland countries with markets for relatively inexpensive products such as dried shark meat. A big problem with chondrichthyan exploitation is that much of the catch is a relatively minor bycatch of fisheries for more fecund teleosts. These teleost fisheries can continue well beyond collapses of cartilaginous fish stocks that are caught by them. Many marine fisheries in developing countries are small-scale and not capital-intensive, but they are collectively massive in their potential impact on cartilaginous fishes because of the sheer number of fishermen participating in the fisheries and the high demand for fisheries products to supplement agricultural and pastoral products for human consumption.

Another problem with these increasing chondrichthyan fisheries is that the fisheries themselves have greatly outstepped biological knowledge of the species involved, even at the level of alpha taxonomy and geographic distribution. Broad trends for catches of individual species are usually not discernible in the catch records of most countries. Only a handful of cartilaginous fishes are well-known biologically, which are mostly fisheries species from temperate coastal waters. Research on sharks, rays, and chimaeras is hampered by the fact that they are a relatively minor catch compared to important bony fish groups and do not command much attention by fisheries biologists in comparison to high-value teleost groups. Little funding exists for the wide-ranging studies necessary to understand enough of the biology of most cartilaginous fishes to make recommendations for regulation of their fisheries. In the meantime the chondrichthyan fisheries are continuing unabated, unstudied, and largely unregulated.

Particularly worrisome fisheries are 1) offshore, deep-trawling operations by international fleets and local directed line fisheries that take poorly known, slow-growing dogfishes and other deep-water chondrichthyans for human consumption, fishmeal, or squalene liver oil; 2) the international sharkfin trade, which targets a low-volume, high-value gourmet product worldwide and fits nicely as a low-risk bycatch for numerous inshore and high seas fisheries; and 3) certain spot fisheries for relatively uncommon, large sharks with exceptionally low fecundity, such as the basking and great white sharks.

The oriental shark-fin fishery seems all-pervasive and may be affecting populations of large oceanic sharks worldwide. Longliners, purse seiners, and pelagic gill-netters can harvest sharkfins as a highly lucrative bycatch with relatively little directed effort and storage problems. By being discarded after removal of their fins, shark carcasses do not compete for freezer space with the more valuable oceanic scombroids that are targeted by such fisheries. The lucrative spot market for the jaws of large great white sharks (*Carcharodon carcharias*) could cause problems for that species, equivalent to those afforded elephants and rhinoceros by the persistent ivory and rhino horn trades. This may also be the case for some species figuring in the sharkfin trade as stocks are depleted and the value of fins continues to rise in the vast oriental market.

There are numerous difficulties in gaining enough knowledge of the biology of exploited species of cartilaginous fishes in order to make recommendations on their management and conservation. Even more troublesome is the actual regulation of chondrichthyan catches by countries engaged in international offshore fisheries that target more valuable teleosts, as well as by developing countries with enormous human populations and widespread undernourishment. Conservation of these fishes may be nearly impossible as fisheries continue to expand, but conservation-minded researchers and international bodies that promote conservation may have to become involved regardless of the difficulties.

Conclusions

World fisheries and shark populations are on a long-term collision course, with sharks as the current and potential victims of overexploitation. The environmental impact of the widespread decimation of sharks and other cartilaginous fishes, many of which are amongst the top marine predators, is unclear. Given the complexity of predator-prey relationships, however, one can predict that the ultimate effect of the removal of these predators will be extensive and negative to marine ecosystems and to humanity. Conservationists and the general public have focused enormous attention on whales and other marine mammals that are threatened by fisheries, but so far nothing comparable has occurred for sharks or other cartilaginous fishes. Public concern, sympathy, interest, and awareness of the problems of shark exploitation and conservation are virtually nil. Research on the general biology, natural history, behavior, ecology, and conservation of sharks and other cartilaginous fishes is minimal and miserably funded, compared to the scope of the difficulties facing these fishes, and needs to be strengthened worldwide.

A persistent problem in certain Western countries is the negative image afforded sharks; the traditional perception of the ''man-eating shark'' hampers shark conservation and promotes expensive ''antishark measures'' and unregulated exploitation. The shark research community should take responsibility for promoting a realistic view of interactions between humans and sharks, and for outlining the far greater danger of humans to sharks.

It is desirable to determine how to regulate fisheries for cartilaginous fishes in order to develop sustainable yields while minimizing the ecological damage of such fisheries. One positive step could be the formation of an international research body of chondrichthyan scientists concerned with rational exploitation and conservation of cartilaginous fishes, analogous to the U.S. Shark Research Panel but with a diametrically opposite approach. Such a body could be responsible for recognizing, compiling, analyzing, and publishing specific data on chondrichthyan fisheries, for promoting research on chondrichthyan biology, management, and conservation, and for making fisheries recommendations in cooperation with FAO, other international organizations, national fisheries commissions, individual fisheries officers and scientists, and other interested parties. It would also highlight vital problems related to chondrichthyan fisheries that needed investigation and would promote research necessary for fisheries management. It would also serve to increase the public's awareness of the sensitivity of chondrichthyans to overexploitation as well as an awareness of the gross imbalance of shark exploitation by humans vs. shark attack on humans. Such a body might maintain an International Shark Exploitation File, a database concerned with trends of fisheries for sharks and other chondrichthyans that would be analogous to the International Shark Attack File. With current funding levels for research, such a proposal may be utopian and quixotic, but the uneven and poor quality of international data on fisheries for cartilaginous fishes and the minimal public awareness of problems with the exploitation of these fishes makes it timely and appropriate.

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The Role of Elasmobranchs in Japanese Fisheries

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ABSTRACT

Elasmobranchs are important food resources for Japanese people. However, Japanese landings of elasmobranchs have shown a gradual decrease in recent years when compared to the constant increase in world elasmobranch catches. Analysis of data for sharks caught by Japanese institutional longline vessels demonstrates that the catch of sharks is about one third of the combined catches of tunas and billfishes. It is estimated that two-thirds of the sharks caught are discarded by the Japanese commercial longline fishery especially on the high seas. The catch per unit effort of pelagic sharks, represented by hook rates per thousand hooks, has been, on the average, constant for the last thirteen years. Twenty-five species of sharks have been reported in the catch of the Japanese longline fishery; *Prionace glauca*, *Isurus oxyrinchus*, *Carcharhinus falciformis*, and *C. longimanus* are the species most frequently caught on the high seas. Elasmobranchs, especially sharks, cause damage to Japanese fisheries by predation on hooked fishes. On the average, approximately eight percent of tunas and billfishes that are caught are damaged by sharks. The annual financial loss due to sharks is estimated to be about ten billion yen in the high seas tuna longline fishery. Elasmobranchs consume vast amounts of prey and may be regarded, in some instances, as competitors that reduce the abundance of certain valuable fisheries resources. It is estimated that eleven to twenty-two million tons of living resources in the world ocean are annually consumed by elasmobranchs.

Introduction

Elasmobranchs are important to the Japanese people in both positive and negative ways. The purpose of this paper is to describe and analyze the role of elasmobranchs in Japanese fisheries, a role that can be defined in three ways (Taniuchi 1984).

First, elasmobranchs are utilized as living resources, whether they are targeted for direct catch or are obtained as a by-catch. Their flesh is consumed fresh, e.g., as sashimi or yubiki, which are popular foods in Kyushu and which are made by soaking the meat in hot water for a very short time. Sometimes the flesh is eaten after boiling and broiling. The dried meat of skates is esteemed as a delicious food in Japan. The meat is also processed into surimi from which is made kamaboko, chikuwa, satsumaage, and hanpen—all popular foods in Japan. Surimi made from sharks has been recently replaced by walleye pollock. Even shark cartilage, when minced with meat, is readily accepted in Japan and is one of several palatable foods called suji. Liver oil is now an important material for expensive cosmetics which are said to smooth and brighten the skin of women. Squalene is also popular as a health food in Japan. Shark skin can be tanned and used for handbags, purses, and belts. Skin from stingrays has been used on the handles of swords because of its nonskid properties. Kreuzer and Ahmed (1978) reviewed the present state of shark utilization and marketing. Some populations of elasmobranchs have been fished to the verge of commercial extinction (Brander 1981; Thorson 1982; Compagno 1984; Anderson 1985; Casey and Hoey 1985). Slow growth and low fecundity can easily lead to a sharp decline if stocks are exploited without management (Holden 1974, 1977).

Second, elasmobranchs, especially sharks, cause damage to fishing gear. Nets are often destroyed because of shark entanglement. The damage caused by spiny dogfish has been discussed by Ketchen (1986). The most serious problem in the tuna longline fishery is that hooked fishes are frequently damaged by shark predation.

Third, elasmobranchs consume a vast amount of prey (Ketchen 1986). They eat large quantities of valuable fishes such as salmon, skipjack, porgy, and tuna resulting in a

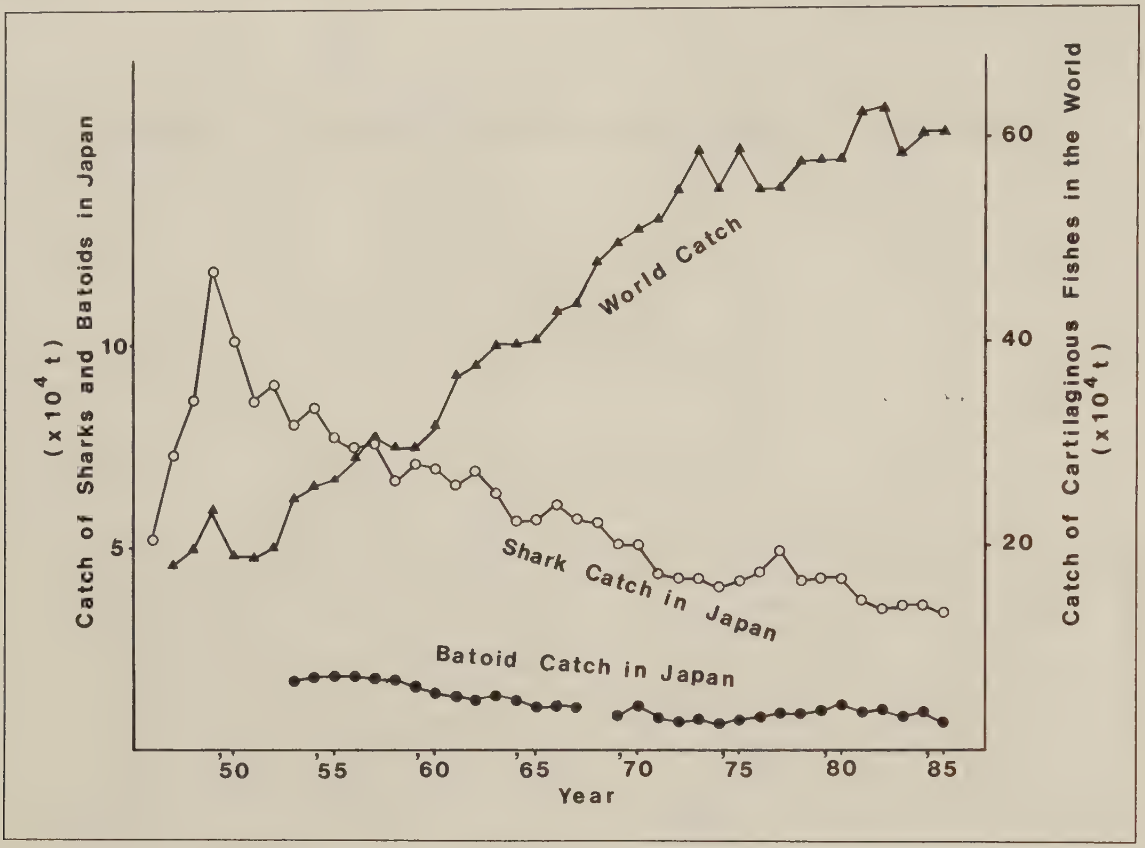

Figure 1.
World catches of cartilaginous fishes and Japanese catches of sharks and batoids. Data from FAO Yearbooks of Fishery Statistics (1950–1985) and Annual Reports of Production Statistics for Fisheries and Aquaculture (1947–1986).

decrease of these populations. They are, in this sense, competing with man (Taniuchi 1984).

Catch and Value of Elasmobranchs

At the present time, there are few major Japanese fisheries directed toward elasmobranchs. For this reason, fisheries statistics are sometimes incomplete. Figure 1 shows world catches of cartilaginous fishes which are mostly composed of elasmobranchs. Catches of sharks and batoid fishes in Japan are also included. According to the FAO Yearbook of Fishery Statistics, from 1950 through 1985, only 200,000 metric tons were caught in the late forties and the early fifties. Actual catches were probably much larger than FAO reports indicated because they varied between and within years and because Japanese landings constituted about half of world catches in 1949. A sharp increase in world landings occurred in 1954 and the catch continued to increase up to 1973. Recent catches are relatively stable, oscillating around 600,000 metric tons. Current world elasmobranch catches could be divided into approximately 350,000 t of sharks, 250,000 t of rays and skates, and less than 10,000 t of chimaeras, judging from FAO statistics. A sharp rise of world elasmobranch catches shown by FAO statistics during the sixties and the early seventies may have been caused by the utilization of elasmobranchs in developing countries and by an apparent increase in the catch due to improvements in recording fishery statistics in each country.

In contrast, the Japanese catch of sharks showed a gradual decline after a peak in the late forties according to The Annual Reports of Production Statistics for Fisheries and Aquaculture (Fig. 1). In the late forties, sharks were caught in large quantities to provide Japanese people with meat and liver oil after World War II. The Japanese shark catch in 1949 amounted to 118,900 t and made up 4.3% of total Japanese fish catches. However, the shark constituted only 0.3% of 1985 total fish catches in Japan. Thus, the relative importance of sharks in Japanese fisheries has shown a considerable decrease during these 40 years. Japanese shark catches in the eighties have varied between 33,000 and 37,000 t. Batoid fishes first appeared in Japanese fisheries statistics in 1953 and showed a peak

Table 1.
Catch in metric tons of sharks caught by Japanese tuna longline fishery for each fishing ground. Data from Annual Reports of Production Statistics for Fisheries and Aquaculture.

		Catches by tuna longline fishery				
Year	Total catch	High seas	Offshore	Coastal	Subtotal	% of total
1976	43,652	7,142	14,167	2,615	23,924	54.8
1977	49,338	6,590	16,352	2,321	25,263	51.2
1978	41,784	7,718	13,189	3,116	24,023	57.5
1979	42,480	8,211	17,025	2,832	28,068	66.1
1980	42,286	8,811	18,639	2,242	29,692	63.1
1981	36,979	8,716	13,623	2,237	24,576	66.7
1982	34,984	8,090	12,567	1,713	22,370	63.9
1983	35,533	9,496	14,025	749	24,270	68.3
1984	35,380	9,009	11,871	2,336	23,216	65.6
1985	33,390	8,042	12,341	2,524	22,907	68.6

Table 2.
Catches in metric tons of tunas and billfishes caught by tuna longline fishery for each fishing ground. Data from Annual Reports of Production Statistics for Fisheries and Aquaculture.

		Catches by tuna longline fishery			
Year	Total catch	High seas	Offshore	Coastal	Subtotal
1976	412,948	181,872	64,668	18,603	265,143
1977	378,078	191,668	75,781	18,674	286,123
1978	431,301	189,269	85,930	19,088	294,287
1979	406,274	193,121	77,143	19,655	289,919
1980	422,616	198,639	84,519	18,746	321,904
1981	407,734	192,747	73,163	15,645	281,555
1982	416,622	206,766	64,052	16,372	287,190
1983	404,968	207,444	67,596	20,435	295,475
1984	413,538	208,959	56,844	20,185	285,988
1985	439,329	220,374	63,194	20,779	304,347

of approximately 19,000 t in 1955. Batoids have shown the same declining trend as sharks (Fig. 1). Annual landings of batoids have been between 6,000 and 9,000 t for the last five years.

Japanese catches of sharks and batoids are inversely proportional to world catches of elasmobranchs. The cause of this decline may be explained by the reduction of Japanese elasmobranch stocks and the decline of their cash value relative to other fishes.

The author has examined the abundance of stocks and the value of elasmobranchs in Japan in order to provide a hypothesis that explains the decline of shark catches. All the data used in Table 1, Table 2, Figure 1, and Figure 2, are derived from the Annual Reports of Production Statistics for Fisheries and Aquaculture published by the Department of Statistics Information (DSI), Japanese Ministry of Agriculture, Forestry, and Fishery (1947–1986). The common and scientific names are shown in Table 3. Since little is known of the abundance of sharks distributed around Japan, catches of the three main species and "other sharks" are presented in Figure 2 from 1951 to 1967 as an index of their abundance. The shark catch has been combined since 1968. In 1949, when shark catches were at a peak, spiny dogfish constituted about two-thirds of the catch. As the total shark catch decreased, the ratio of spiny dogfish to the total showed a sharp decrease. On the other hand, the blue shark landings remained stable and the salmon shark landings decreased to half of the 1951 catch. The reduction of spiny dogfish landings affected Japanese shark catches while pelagic sharks, like the blue shark, had little influence on them. Spiny dogfish stocks are vulnerable to recruitment overfishing and were reported to undergo a large decline in the northeastern Atlantic (Ketchen 1986). Spiny dogfish are demersal and caught with bottom trawls; whereas pelagic sharks, like the blue shark and the salmon shark, are widely distributed and caught with longline gear. It is very probable that bottom fishing can easily reduce the stocks of spiny dogfish. Judg-

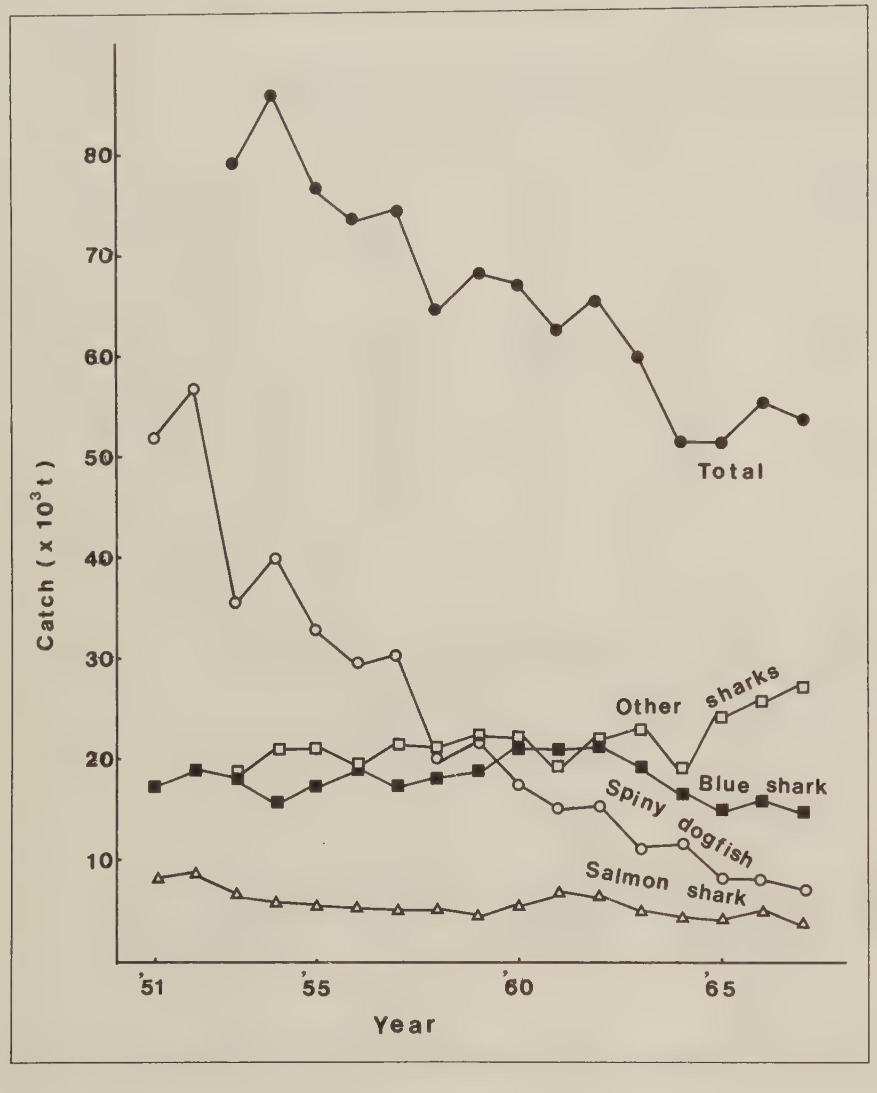

Figure 2.
Commercial catches of spiny dogfish, blue sharks, salmon sharks, and other sharks from 1951 to 1967 in Japan. Data from Annual Reports of Production Statistics for Fisheries and Aquaculture.

Table 3.
Species names of sharks captured by Japanese tuna longline vessels.

Common name	Scientific name	Source
Crocodile shark	*Pseudocarcharias kamoharai*	Taniuchi (1979)
Sand tiger	*Eugomphodus taurus*	Taniuchi (1970)
Salmon shark	*Lamna ditropis*	Taniuchi (1979)
Porbeagle	*L. nasus*	Taniuchi (1979)
White shark	*Carcharodon carcharias*	Taniuchi (1979)
Shortfin mako	*Isurus oxyrinchus*	Taniuchi (1979)
Longfin mako	*I. paucus*	Taniuchi (1979)
Bigeye thresher	*Alopias superciliosus*	Taniuchi (1979)
Thresher shark	*A. vulpinus*	Taniuchi (1979)
Pelagic thresher	*A. pelagicus*	Taniuchi (1979)
Tiger shark	*Galeocerdo cuvier*	Taniuchi (1979)
Blue shark	*Prionace glauca*	Taniuchi (1979)
Narrowtooth shark	*Carcharhinus brachyurus*	Unpublished
Spinner shark	*C. brevipinna*	Unpublished
Silky shark	*Carcharhinus falciformis*	Taniuchi (1979)
Galapagos shark	*C. galapagensis*	Taniuchi et al. (1985)
Blacktip shark	*C. limbatus*	Unpublished
Oceanic whitetip shark	*C. longimanus*	Taniuchi (1979)
Dusky shark	*C. obscurus*	Taniuchi (1979)
Sandbar shark	*C. plumbeus*	Taniuchi (1971)
Scalloped hammerhead	*Spyrna lewini*	Taniuchi (1974)
Great hammerhead	*S. mokarran*	Taniuchi (1974)
Smooth hammerhead	*S. zygaena*	Taniuchi (1974)
Velvet dogfish	*Scymnodon squamulosus*	Unpublished
Whitetail shark	*Symnodalatias albicauda*	Taniuchi and Garrick (1986)

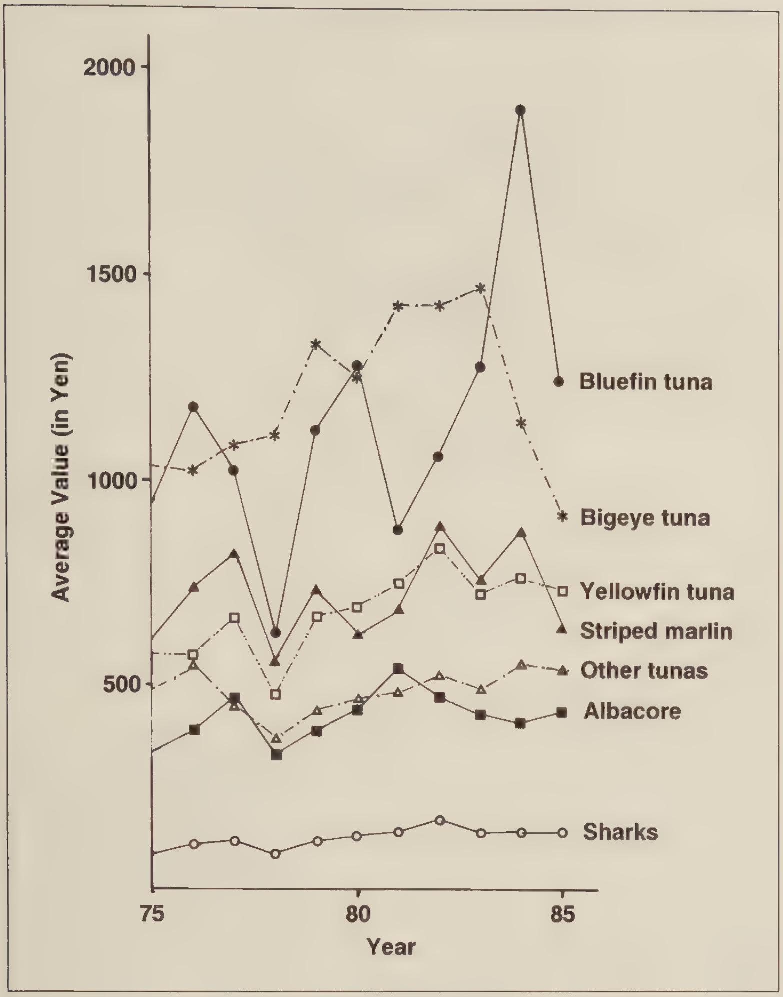

Figure 3.
Annual average values (in yen) of sharks, batoids, and total fishes caught in Japan. Data from Annual Reports of Circulation Statistics for Fisheries and Aquaculture.

ing from the tendency shown in Figure 2, the recent decline of Japanese shark catches may be largely ascribed to a sharp reduction of the spiny dogfish stocks.

Annual average value of elasmobranchs, compared to the total fish landed in Japan, are shown in Figure 3. Data are obtained from the Annual Reports of Circulation Statistics for Fisheries and Aquaculture, published by DSI (1967–1986). In the 1960s and the early 1970s, the average value of sharks and batoids was lower than that of total fishes. A sudden rise occurred in the early 1970s with the onset of the first increase in the price of commercial oil. The values continued to rise until 1982. From 1983 on, sharks and batoids have exceeded total fishes in value. Higher values of elasmobranchs may give the impression that they will be of high commercial value as a fishery. However, the total average value is largely influenced by the low price of sardines which make up one-third of the total Japanese catches.

To determine if elasmobranchs are utilized efficiently, that is, whether or not they are brought back to port when caught, it is important to know what kind of gear captures them. The catch of sharks, tunas, and billfishes is shown for the tuna longline fishing method in Table 1 and Table 2. Sharks make up about two-thirds of the catch. The price of sharks and other fishes caught by longline can be compared graphically in Figure 4. It is clear that any species of tuna or billfish has a higher value than sharks. Even albacore, the least expensive of all tunas, is three times higher in price than sharks. The price of sharks was one-tenth of the price of bluefin tuna, the most expensive of the tunas, in 1985. Many longline caught sharks are currently returned to the sea because of their low value and difficulty in handling at the rail.

To determine if longline caught sharks are in fact landed when they are caught by commercial vessels, I used the catch records of longline vessels belonging to fisheries schools and prefectural fisheries experimental stations (referred to in the text as "institutional" vessels). These vessels fish in areas defined by the Far Seas Fisheries Research Laboratory (Fig. 5) and are required to report their catch and oceanographic information to the Far Seas Research Laboratory which publishes them in the Proceedings of the Tuna Fisheries Research Conference. From these catch data, which may contain inaccuracies, I

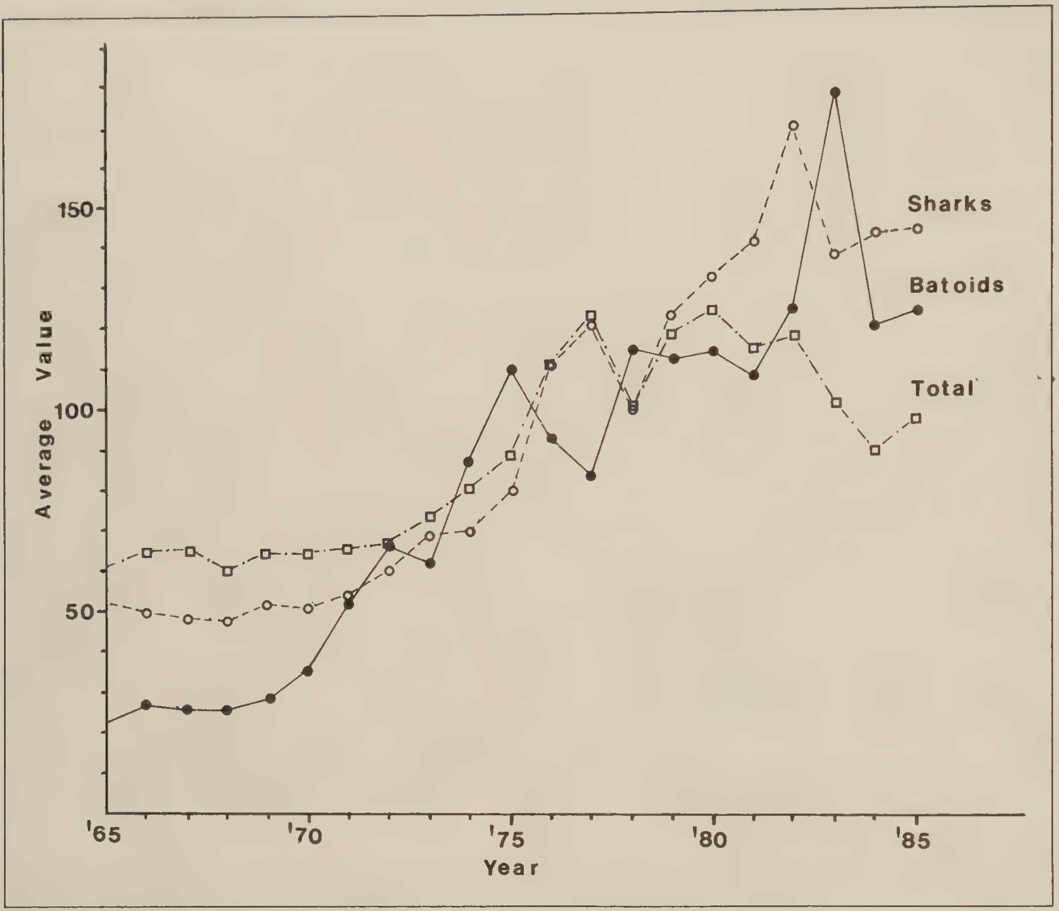

Figure 4.
Annual average values (in yen) of sharks, tunas, and billfishes landed in Japan. Data from Annual Reports of Circulation Statistics for Fisheries and Aquaculture.

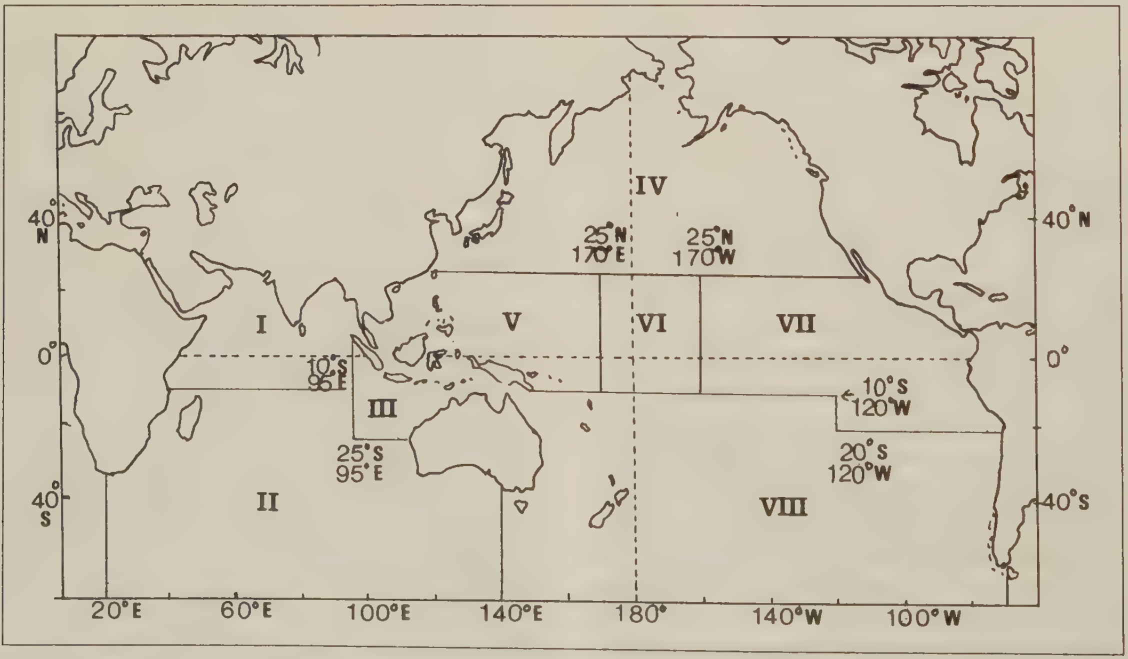
IV
25°N 170°E
25°N 170°W
I
V
VI
VII
10°S 95°E
III
10°S 120°W
25°S 95°E
20°S 120°W
II
VIII
40°N
0°
40°S
40°N
0°
40°S
20°E
60°E
100°E
140°E
180°
140°W
100°W

Figure 5.
Fishing areas used by Japanese institutional tuna longline boats as defined by Far Seas Fisheries Research Laboratory, Japan.

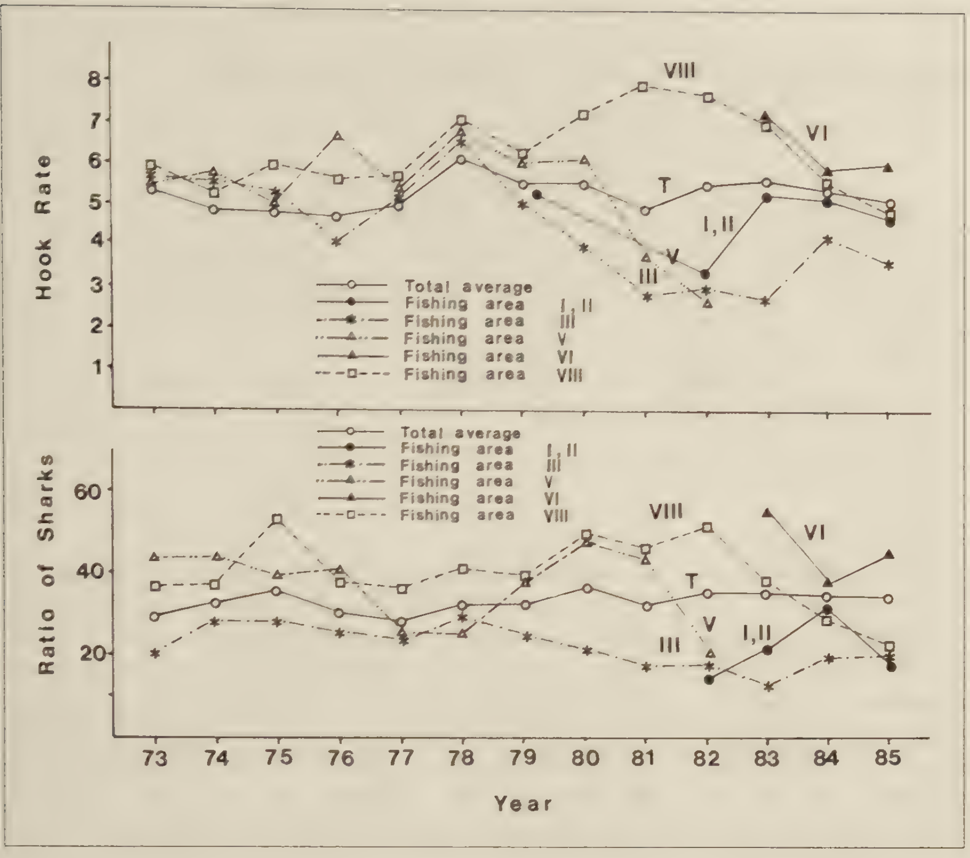

Figure 6.
Ratios of shark catch to catches of tunas and billfishes and hook rates of sharks expressed by number of sharks caught per thousand hooks. Catch data were obtained from the Proceedings of Tuna Fisheries Research Conference. Roman numerals refer to fishing areas (see Fig. 5). "T" indicates a total overall average.

calculated the ratios of sharks to tunas and billfishes and the number of sharks captured per thousand hooks (Fig. 6). Longline vessels were concentrated in fishing areas III, V, and VIII until 1982. After 1983, the main fishing area was VII. Although the ratios and hook rates differed between fishing areas, i.e., high in VII and VIII and low in I, II, and III, the average ratio for these 13 years was approximately 30% overall. If we assume that commercial fishing vessels capture sharks in the same proportion as shown in institutional fishing vessel records, and that individual weight is not different between sharks and tunas, then the catch of sharks must be nearly identical to the catch of tunas and billfishes (30%). Since about 300,000 t of these fishes are caught in the tuna longline fishery, the total reported and unreported shark catch is estimated at roughly 90,000 t. Even if the above assumption is applied to the high seas longline fishery, the shark catch should be 30% of the tuna and billfish catches of approximately 220,000 t as shown in Table 2, that is, 66,000 t in the high sea longline fishery. However, the catch of sharks is reported to be only 23,000 t in the total longline fishery and 8,000 t in the high seas longline fishery (Table 1). The difference between reported and estimated catches suggests that a considerable number of sharks are returned to the sea unprocessed. The author's discussions with commercial longline fishermen reveal that most sharks that are hooked are usually discarded. Thus, sharks are not used in the Japanese longline fishery because of their low price in comparison to tunas and billfishes and because of the danger they pose to fishermen when they are boated.

Hook rates have been nearly constant for the last 13 years, although the hook rate values vary between fishing areas (Fig. 6). Hook rates average about five sharks per thousand hooks. Since hook rates are generally considered to be an index of density, the abundance of sharks seems to have been fairly constant over these 13 years. However, hook rates are changing in some fishing areas. Hook rates in area VIII (Fig. 5) have gradually decreased since 1981, though absolute values were higher than in any other area. In 1984 and 1985, the number of operations decreased in area VIII, while it increased in area VI where hook rates were high. The total hook rates for sharks in the present study are almost identical to those in the Atlantic U.S. Fishery Conservation Zone (Witzell 1985). However, they are a little lower than those for sharks in the Indian Ocean (Pillai and Honma 1978).

A total of 25 shark species have been recorded by Japanese longline fishermen (Table 3). Specimens of most of these species have been preserved in the University Museum of the University of Tokyo. Among these sharks, seven species were caught chiefly on the high seas: *Prionace glauca*, *Carcharhinus longimanus*, *C. falciformis*, *Isurus oxyrin-*

Table 4.
Species composition of sharks caught by some institutional tuna longline vessels operating from 1967 to 1968 in the open sea.

	Number (percentage)		
Species	Indian Ocean	Western Pacific	Eastern Pacific
Prionace glauca	2724 (76.6%)	2153 (46.5%)	1039 (41.5%)
Isurus oxyrinchus	231 (6.5%)	134 (2.9%)	171 (6.8%)
Carcharhinus falciformis	234 (6.6%)	581 (12.5%)	666 (26.6%)
Carcharhinus longimanus	121 (3.4%)	1042 (22.5%)	533 (21.3%)
C. falciformis and *C. longimanus*	54 (1.5%)	483 (10.4%)	
Other sharks	190 (5.3%)	241 (5.2%)	92 (3.7%)
Total	3554	4634	2501

chus, *I. paucus*, *Pseudocarcharias kamoharai*, and *Alopias superciliosus* (Taniuchi 1979).

The species composition of sharks, obtained from logbook records of some institutional tuna longline vessels operating from 1967 to 1968, was investigated (Table 4). Fishing grounds were arbitrarily divided into three regions: Indian Ocean, western Pacific, and eastern Pacific. The eastern and the western Pacific were divided by the international date line. In the Indian Ocean, *Prionace glauca* was most abundant because the target species in the fishery was the southern bluefin tuna which is distributed in cooler waters. In the western Pacific, percentages of *Carcharhinus longimanus* and *C. falciformis* were relatively high after *P. glauca*, which made up half of the catch. *Carcharhinus longimanus* and *C. falciformis* were combined when the two species could not be separated from logbook records. In the eastern Pacific, *P. glauca* comprised only 40% of the catches, while *C. longimanus* and *C. falciformis* represented 20% of the catches, respectively. Four species, namely *P. glauca*, *C. longimanus*, *C. falciformis*, and *Icurus oxyrinchus*, comprised over 90% of the total shark catch in all regions. The result of this study agrees well with reports from the central Pacific by Strasburg (1958) and from the eastern Pacific by Sibasubramaniam (1965).

Damage to the Commercial Catch by Sharks

Little is known of the financial loss to Japanese fisheries caused by elasmobranchs. An investigation into the damage caused by sharks (Anon 1978) showed that eight types of fishing gear are affected. These include longline, pole and line, setnets, gill nets, purse seines, and trolling gear. The kinds of fishes frequently damaged were billfishes, skipjack, and flying fishes in the pelagic zone; yellowtail, squid, and hairtail in the bathypelagic zones; and many demersal fishes in the benthic zone. The loss to fisheries caused by sharks was approximately 100–1,000 million yen in each region. Several species of carcharhinids, consisting of blue and hammerhead sharks, caused much of the damage to the commercial catch. In the Izu Islands and Bonin Islands, fisheries for flying fishes suffered from predation by sharks. The investigation (Anon 1978) concluded that the best way to protect gear and the catch from sharks was to deplete the shark population by fishing.

Problems of shark and killer whale predation on hooked tunas and billfishes are much more serious in the pelagic fisheries. Sivasubramaniam (1965) reported investigations of predation by killer whales. Predation by sharks has been reported by Sivasubramaniam (1963, 1965), Hirayama (1976), and Kobayashi and Yamaguchi (1978). Hirayama (1976) pointed out that the percentage of damaged tunas and billfishes varies between regions and is high in the eastern Pacific (14.45%), in the central Pacific (10.16%), and in the western Pacific (10.46%) while it is low in the Coral Sea (4.78%), in the tropical Indian Ocean (4.31%), in the Indian Ocean adjacent to Australia (4.37%), and in the sea around Madagascar (1.64%). Kobayashi and Yamaguchi (1978) reported that the average damage to tunas and billfishes is 7.5% of the total catch in the equatorial region of the eastern Pacific. Their average value of percentage damage is a little lower than a weighted mean of 8.8%, calculated from Hirayama's (1976) data by the author. Kobayashi and Yamaguchi (1978) also stated that there is a correlation between percentage of damage and density of sharks as expressed by hook rates. However, other data (Taniuchi, unpubl.) do not support existence of a correlation between percent damage and percent density (Fig. 7). This diagram suggests that there is no special relationship between the two factors. Percent damage for each five degrees of latitude (author's data) is shown in Table 5. The percent damage showed a gradual decrease with increasing latitude. Since the percent damage in this table excludes damaged tunas from the denominator, the percentages are a little higher than those of Hirayama

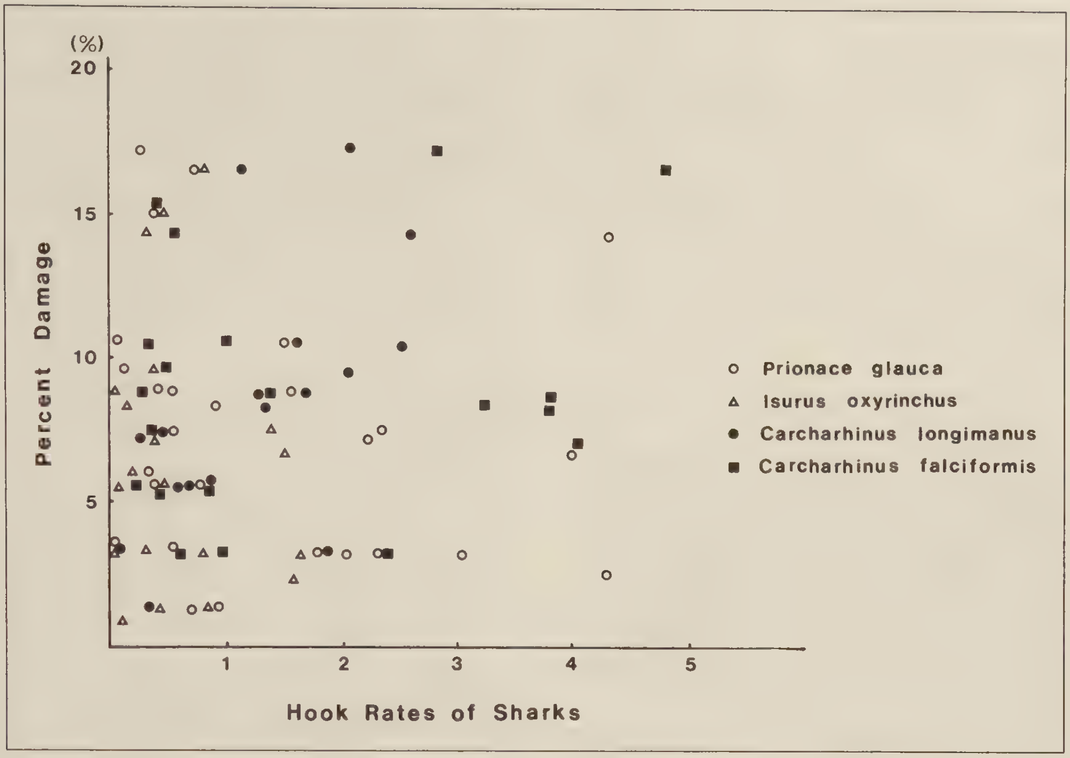

Figure 7.
Relationship between percent damage of tunas and billfishes (combined) and hook rate of each shark caught by institutional tuna longline boats.

Table 5.
Frequency distributions of percent damage to tunas and billfishes (together) caused by sharks at 5° latitude intervals. Data were provided by institutional tuna longline vessels operating from 1967 to 1968.

	Frequency of percent damage					
Latitude	0-5.0%	5.1-10.0%	10.1-15.0%	15.1-20.0%	>20.1%	Total
<15°N	2	—	—	—	—	2
10-15°N	11	3	—	—	—	14
5-10°N	11	9	6	6	3	35
0-5° N	15	15	15	9	2	56
0-5° S	—	2	—	—	—	2
5-10°S	13	11	—	—	—	24
10-15°S	9	4	3	3	1	20
>15°S	26	1	—	—	—	27
Total	87	45	24	18	6	180

(1976) and Kobayashi and Yamaguchi (1978). If the percent damage is changed according to their calculations, my average of 7.9% fits as an intermediate value between the results of the two studies.

If we assume that the average damage to tunas and related species is about 8%, then it is estimated that 24,000 t of these fishes are damaged by sharks, since the catch of the tuna longline fishery is approximately 300,000 t. Considering that these calculations of damage are confined to the high seas fishery, about 18,000 t of tunas are damaged by predation. The total value of tunas and billfishes is about 390 billion yen. As 70% of these fishes are caught by the tuna longline fishery, the total value of tunas and billfishes is about 270 billion yen. Therefore, eight percent of

Table 6.
Frequency of percentage occurrence of empty stomachs in four main species of pelagic sharks caught by tuna longlines. Data were provided by institutional tuna longline vessels operating from 1967 to 1968.

	Frequency of percent empty stomachs						
Species name	<50%	50.1-60.0%	60.1-70.0%	70.1-80%	80.1-90%	90.1-100%	Total
Prionace glauca	—	2	3	5	6	10	26
Isurus oxyrinchus	1	1	2	3	1	4	12
Carcharhinus falciformis	—	—	—	1	2	15	18
Carcharhinus longimanus	2	—	1	1	2	18	24
Total	3	3	6	10	11	47	80

270 billion, or 21.6 billion yen is lost to shark damage. In the case of the high seas fishery, a loss of about 10 billion yen is caused by sharks. Since meat damaged by sharks is used for canning and fish sausage, all damaged fish can not be considered to be completely lost. However, it is highly probable that loss due to predation by sharks may exceed the gain made from the catches of sharks (about 6 billion yen).

Predation on Marine Organisms

Elasmobranchs, as apex predators, consume large quantities of prey and, in some cases, may be considered to be competitors with man. Spiny dogfish, in British Columbia waters, consumed 230,000 tons of herring annually (Jones and Geen 1977). This figure was nearly equal to the all-time record annual harvest, although it was considered to be an overestimate by Ketchen (1986). The Japanese swellshark consumes 71 species of prey, chiefly fishes (Taniuchi 1988); about one-third of which is potentially marketable. Sometimes six or seven species are found in stomach contents of the swellshark and occupy 20% of their total body weight. Empty stomachs seldom occur. On the other hand, in the case of pelagic sharks caught on longline gear, more than 90% of the sharks have empty stomachs (Table 6). Percentages of empty stomachs for four common species of pelagic sharks were calculated on the basis of data from institutional tuna longline vessels. All species showed high percentages of empty stomachs, especially *Carcharinus falciformis*. In *Isurus oxyrinchus*, the percentage was relatively low. The same phenomena were also reported by Backus et al. (1956), Strasburg (1958), Sano (1962), Stevens (1973), and Wass (1973), although the percentage of empty stomachs was relatively low in the latter three cases. Three plausible explanations for a high occurrence of empty stomachs are possible: first, sharks with full stomachs do not take a bait, while sharks with empty stomachs are more likely to be caught because of their hungry condition; second, sharks regurgitate stomach contents after being hooked, a fact which is supported in part by the evidence that stomachs of longline caught sharks are frequently found distended towards their mouth; third, the need for continual feeding is unnecessary because sharks require very little nutrition for maintenance. Perhaps the three factors together lead to the high occurrence of empty stomachs.

Predation by elasmobranchs on useful fishes is a serious problem in some areas. Investigations into predation on salmon in the north Pacific (Sano 1962) showed that a considerable number of salmon were attacked by the salmon shark, *Lamna ditropis*. There were no basic differences in stomach contents between sharks caught by longlines and drift nets, but the percentage of empty stomachs was higher in sharks caught by longlines than in sharks caught by drift nets. The overall percentage of occurrence of salmon in the stomachs of *L. ditropis* was 22%. Sockeye, chum, coho, and humpback salmon showed a high occurrence in that order. Sano (1962) also reported that the usual number of salmon per shark stomach was two or three; but, in an extreme case, eight salmon were found in a shark. Occurrence of other fishes, like walleye pollock, was also relatively high as was the occurence of squid. Sano (1962) also pointed out that there is a correlation between the catches of salmon and sharks. Thus, it is probable that sharks reduce the abundance of salmon populations and thus decrease the number of salmon available to fisheries. Similarly, pelagic sharks in open waters are possibly competitors with man. *Prionace glauca* feeds on squid and octopus most frequently (40% by occurrence) (Taniuchi 1984). They also prey on tunas and cutlassfish, *Trichiurus leptus*. Albacore tuna is preferred, which may explain shark occurrence in high latitudes where albacore is abundant. *Isurus oxyrinchus* also preys on tunas and skipjack (70% by occurrence) which reflects the high level of activity and voracious appetite of the shortfin mako shark. *Carcharhinus falciformis* was reported by Backus et al. (1956) to have driven *C. longimanus* out of coastal waters and into oceanic regions where prey is less abundant. The fact that *C. falciformis* feeds on tunas (48.4%) and skipjack (22.6%) supports the idea of their speed and agility suggested by Backus et al. (1956). Thus, four species of sharks show a high frequency of occurrence of tunas and related fishes in their stomachs. It is not clear whether they feed primarily on living or dead fishes. *Carcharhinus longimanus*, the most sluggish shark among the four species, was reported to feed on living tuna by Bullis (1961); it is possible that these sharks do eat living tunas and related species. However, it is necessary to consider the influence of other factors such as the shark population size, species, and the natural mortality of prey, excluding predation by sharks, to elucidate the effect of predation by sharks on fish such as salmon and tunas.

Last, I will try to show the total amount of prey consumed by elasmobranchs each year. For this calculation, it is necessary to know how many elasmobranchs exist in the sea. The standing stock is first estimated using Baranov's catch equation (Ricker 1977):

$$\frac{C}{N} = \frac{F}{(F+M)}(1 - e^{-(F+M)}),$$

where C is the number of fish caught; N is the population at the start of the year; F is the instantaneous coefficient of fishing mortality; and M is the instantaneous coefficient of natural mortality. In the case of Scottish–Norwegian stock of spiny dogfish, Holden (1968) gave $M = 0.1$ and $F = 0.187$ from six years of age onwards. If we use these values, an $N = 6.2 \times C$ is obtained. Holden (1968) showed that the reproductive rate of the spiny dogfish stock was too low (0.44) to replace the stock. If the F is lowered to 0.1, then $N = 11.0 \times C$ is obtained. $N = 11.0 \times C$ means that the size of the stock of elasmobranchs is eleven times larger than the size of the catch at the start of the year. If we assume that the weight distribution of the catch reflects that of a natural population, the weight of the stock is ten times heavier than the catch at the end of the year. Worldwide catches of elasmobranchs were roughly 600,000 t in 1985. Therefore, approximately six million tons of elasmobranchs existed during 1985. Parameters used here were estimated twenty years ago and may not reflect the state of the present population. Furthermore, parameters for spiny dogfish may not apply to other elasmobranchs, especially pelagic ones. I used them on a trial basis since, at present, both fishing and natural mortalities have not been given for any species of elasmobranchs, so far as I know.

Daily ration, represented as a ratio of body weight to food weight, has been estimated for various sharks, e.g., 0.4–2.0% for sharks in general (Clark 1963), 2.7% for the young lemon shark (Gruber 1982), 3.2% for the shortfin mako (Stillwell and Kohler 1982), 0.56% for the blue shark (Kohler 1987), and 1% for the sandbar shark (Medved et al. 1988). If we postulate that predators eat 1% of their body weight per day, then we calculate that they will eat 3.65 times their body weight per year. If we extrapolate this calculation to all elasmobranchs in the world ocean, then six million t × 3.65 equivalent prey will be consumed per year or 21.9 million metric tons. If we lower the daily ration to 0.5%, annual consumption of prey by elasmobranchs would be approximately 11 million metric tons.

It should be borne in mind that most prey consumed by elasmobranchs are not available to mankind, although predation on some valuable species in some places is a serious problem for fishermen.

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Shark Fisheries in Mexico: The Case of Yucatan as an Example

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ABSTRACT

Fishing for sharks in Mexico has been a traditional activity for many decades, but little has been done to rationally manage these fisheries. Studies leading to management of the shark fishery of Yucatan, Mexico, were begun in 1984 at the Instituto Nacional de la Pesca. Because no prior information was available on the shark populations under exploitation, the first step has been to determine species composition of the commercial catches, as well as meristics and population structure of the important species. A survey of fishing units used in the local fishery is reported. These can be divided into vessels which fish only for sharks and those which target other species of fishes and land sharks as a bycatch. To date, 25 different species of sharks have been recorded, with five carcharhinids, one sphyrnid, and one triakid being the most important shark species in the Yucatan fishery. Length frequencies and length-weight relationships for these species are given.

Introduction

Mexico is a country with more than 10,000 km of coastline bordering an Economical Exclusive Zone of almost 2,000,000 km^2; thus Mexico has a great potential for exploiting fishery resources of many kinds. The commercial exploitation of sharks as a marine resource has been a tradition for mexican fishermen for many decades. The uses given to sharks in Mexico vary from leather industries and fin exportation to their use as food in many very popular dishes.

According to FAO 1985 statistics, Mexico is fourth in the world in shark fishing (Secretaria de Pesca 1988). Unfortunately, despite the importance of Mexican shark fisheries for world shark production, nothing has been done towards managing Mexico's shark fisheries, mainly because of the lack of knowledge about their biology, ecology, and fisheries management.

The fisheries biology of sharks has not received significant attention among scientists, not only in Mexico, but also in the rest of the world, and much is yet to be done in this field. As an example, to our knowledge, the only other ongoing study concerning management of a commercial shark fishery is the study of the blacktip (*Carcharhinus tilstoni*) fishery off the Northern Territory in Australia (Stevens and Wiley 1986), although some fishery management directed efforts are being made off the east coast of the United States (Hoff and Musick 1990).

The purpose of this report is first to give a background of the importance of sharks to Mexican fisheries and specifically to the Yucatan fishery, and second to present the results achieved in the first part of the Yucatan study, which will hopefully lead to the rational exploitation of sharks as a living resource for Mexico.

Methods

Three different sources of data have been used. All information regarding shark landings and their economical value was obtained from official statistics of the Mexican government published through the Ministry of Commerce and Industry, Ministry of Budget and Programation, and the Ministry of Fisheries, and condensed in fisheries yearbooks. Unfortunately only catch data were available, so a CPUE analysis could not be performed.

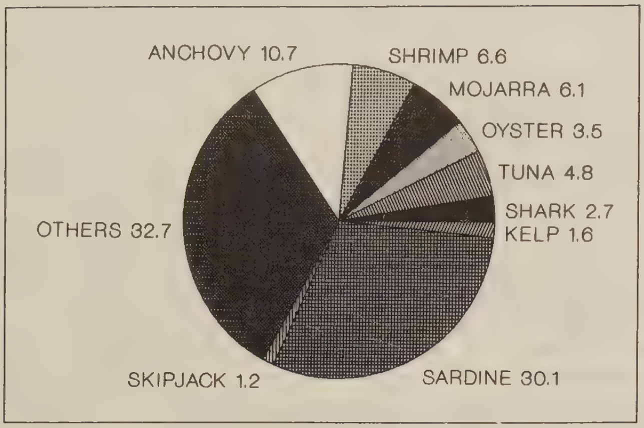

Figure 1.
Principle resources fished in Mexico, as percentage of the total fished weight, for the years 1983–1985.

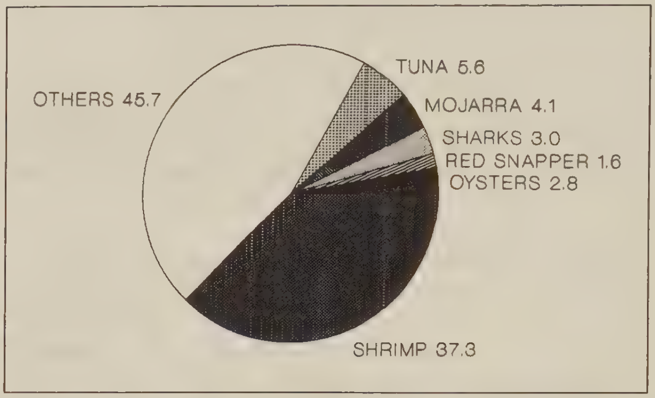

Figure 2.
Principle resources fished in Mexico, as percentage of the total income produced by fishing activities, for the years 1984 and 1985.

In order to estimate the relative importance of sharks in Mexican fisheries and the extent of their contribution to the total, the major fisheries in Mexico were analysed by live (round) weight and by economic value. Historical records of Yucatan shark catches, from 1956 to 1985 were analysed to determine trends in the fishery. Local custom divided the catches into two size categories, "cazon" and "shark". "Cazon" are sharks less than 1.5 m total length (TL) whether they are a small species or a juvenile member of a large species. The term shark alternately refers to all sharks longer than 1.5 TL. Catch composition was analysed by the numbers of individuals of each species sampled and by total weight. Weight samples were separated into two size groups according to maximum reported size for each species, in order to avoid any bias due to differences in average weight between large and small species.

All data concerning the shark populations, and part of the data from fishing units and grounds, have been gathered directly from the field. We used continuous commercial catch sampling at the most important fishing ports of Yucatan and to a lesser extent shark fishing cruises made on Instituto Nacional de la Pesca (I.N.P.) research vessels. Sharks were identified, sexed, and measured in total length following Compagno (1984). Sharks bigger than 1.5 m TL are always landed whole in order to process their skins, whereas smaller sharks are gutted at sea most of the time. Total weights were obtained when possible; gutted (dressed) weights were taken on small sharks when sampled in port.

Results and Discussion

Sharks and Fisheries in Mexico

Mexico's seven most important resources by weight for the period 1983–1985 were sardine, anchovy, shrimp, mojarra, tuna, shark, and kelp, with shark accounting for 2.7% of the total weight from all fishery resources (Fig. 1). For the years 1984 and 1985, an analysis of income produced by the six most valuable resources in Mexican fisheries showed shark as the fourth most important with 3% of the total income from fishing activities and was only surpassed by species such as shrimp, tuna, and mojarra (Fig. 2).

Although shark did not occupy a first rank place in either of the two cases analysed above, and even though it is obviously not a major fishing activity in Mexico, it is clear that sharks are an important secondary resource to Mexican fishermen along with tuna and mojarra. The importance of the shark fishery grows when we consider the added value of shark by-products, such as flesh, fins, skin, jaws and teeth, and offal which is reduced to fish meal by burning.

Shark fishing activities were widespread along the Mexican coast from 1983–1985. Each of the four major fishing zones had approximately the same percentage of landings (Fig. 3). The states where most shark fishing was conducted are shown in Table 1. Yucatan ranks 7th by catch weight in a total of 14 states fishing for sharks. Yucatan is therefore a typical state in the Mexican shark fishing industry.

Sharks and Fisheries in Yucatan

The relative importance of Yucatan's major fisheries by weight, is shown in Figure 4. Shark accounted for 6.5% of the total weight and was the fourth most important fishery preceded by red grouper, octopus, and sardine, and followed by king mackerel and mojarra. Sharks were also fourth in producing income preceded by red grouper, octopus, and shrimp (Fig 5). Shark is one of the most important secondary fisheries in the State of Yucatan, as well as in all of Mexico.

The Yucatan fishery has had three different periods in its evolution (Fig. 6). The first was a slow but sustained

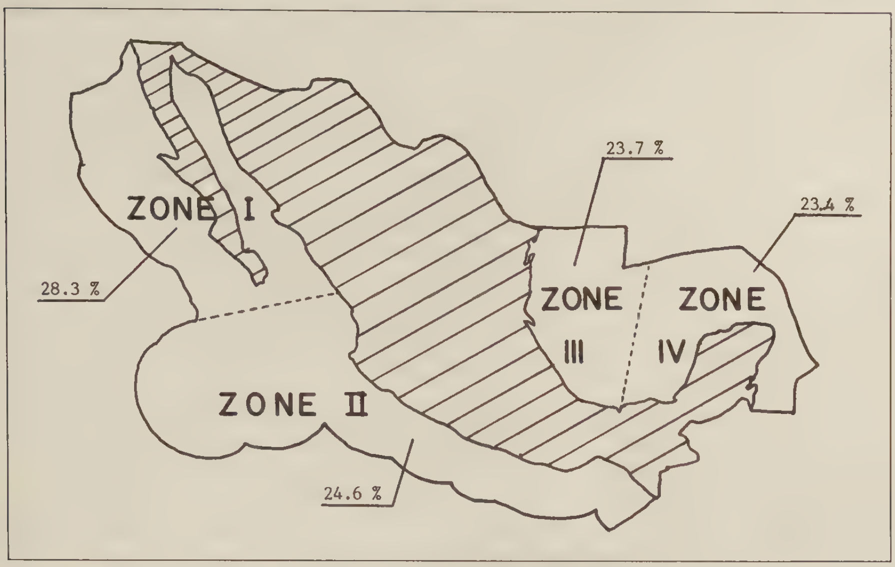

Figure 3.
Main fishing zones in Mexico showing their contribution to the total shark catch (1983–1985).

Table 1.
Landings of the main shark fishing States of Mexico for the period 1983–1985 in metric tons.

	Landings in metric tons			
Fishing States	1983	1984	1985	Mean landing
Veracruz	4,212	5,566	4,761	4,846
Sonora	4,050	4,654	5,292	4,665
Chiapas	2,781	3,978	4,183	3,647
Campeche	3,754	3,844	2,532	3,377
Northern Baja	3,379	2,178	1,600	2,386
Southern Baja	2,535	2,167	2,438	2,380
Yucatan	2,351	2,074	2,361	2,262
Other 7 States	7,259	8,512	8,214	7,995

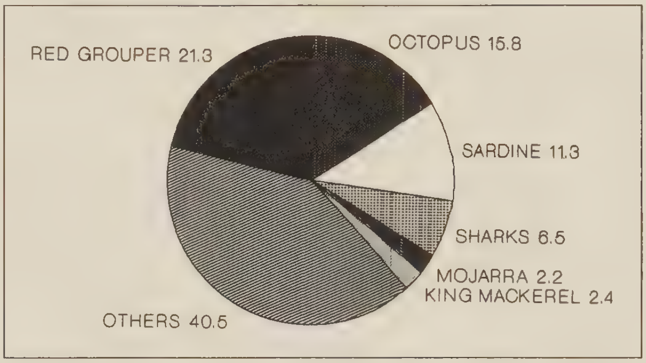

Figure 4.
Principle resources fished in Yucatan, Mexico, as percentage of the total live weight, for the years 1983–1985.

growth period from 1956 to 1971, which was followed by a second period of lower catches with fluctuations until 1979. From 1980 on, there was a third period of explosive growth of the fishery when catches exceeded more than 2,000 t in 1982 and which have been maintained around 2,220 t/year since then. Preliminary information indicates an increase in the number of boats fishing for sharks is responsible of this last situation. Until now, there is no evidence of overexploitation of sharks, but any attempt to increase shark catches must be done with caution to prevent a sudden collapse of the fishery, as has happened with other shark fisheries after a short period of intensive effort (Holden 1977; Anderson 1990).

Yucatan has eight major fishing ports along its coast. The port of Progreso is the most important because it can accommodate ships with a draft of up to 3 m. About 60% of the total fish-processing industry in the state is located in Progreso. The contribution of each port to the total shark

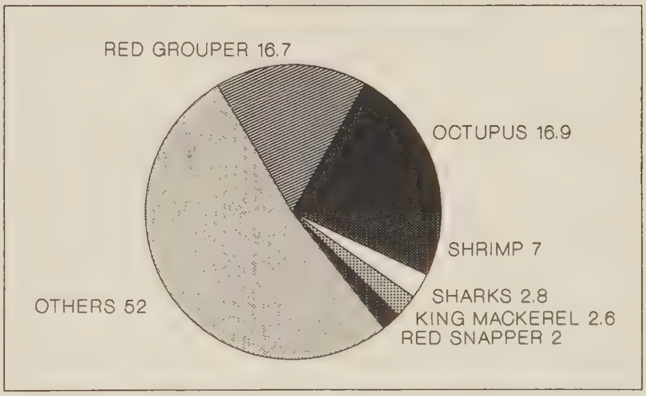

Figure 5.
Main economic fishery resources of Yucatan, Mexico by the percentage of total income from fishing activities, for the years 1983–1985.

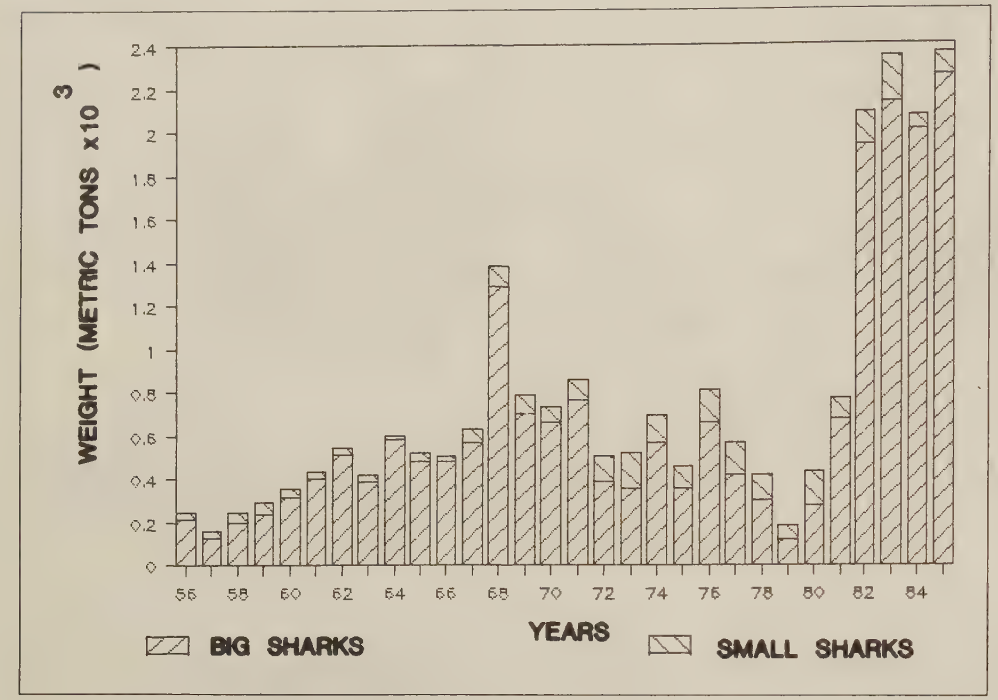

Figure 6.
Total weight of commercial shark catches from Yucatan, Mexico, between 1956 and 1985.

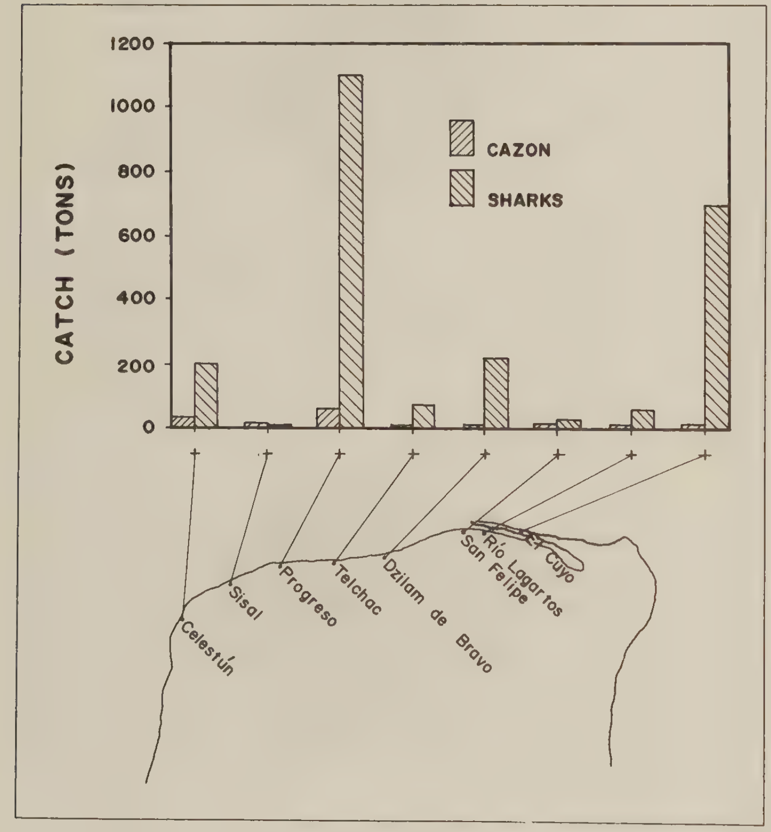

Figure 7.
Mean catch of sharks for the years 1983-1985 made by each fishing port of Yucatan, Mexico.

catch for the years 1983-1985 (Fig. 7) showed Progreso to be the principal port accounting for half the total catch of both shark and cazon. The remaining half of the shark catches were landed mainly at El Cuyo, Dzilam de Bravo, and Celestun, with the remaining four ports having very small landings of sharks. For "cazon" catches, Celestun was second to Progreso, the remaining six ports all had insignificant catches.

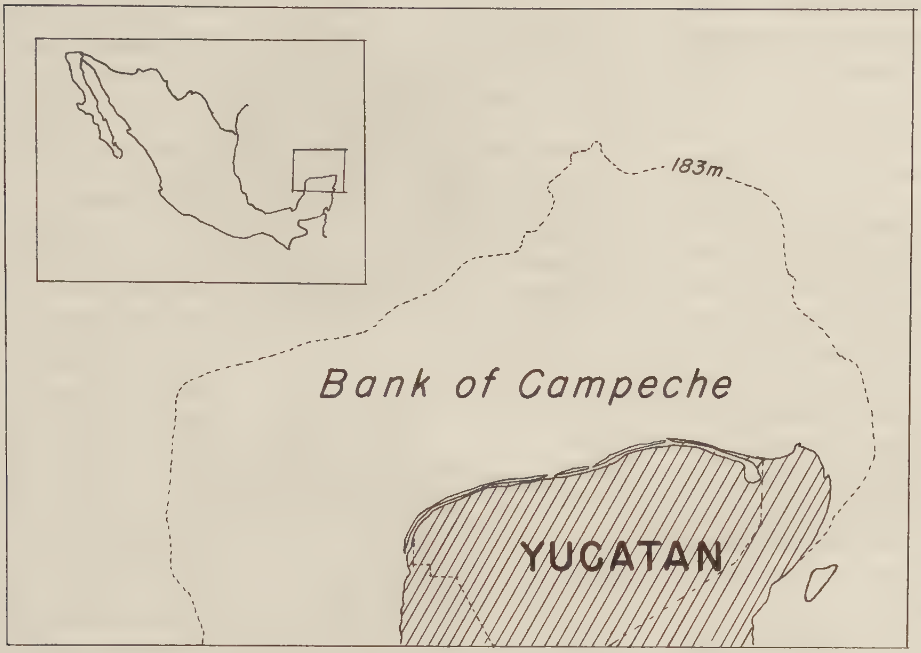

Figure 8.
State of Yucatan and Bank of Campeche showing 183 meters isobath.

Table 2.
Types of fishing units used in the shark fishery of Yucatan, Mexico.

Fishing category	Type of vessel	Length (m)	Fishing gear
Directed	Fiberglass boat with inboard motor	10–13	Shark gill net
Directed	Fiberglass or wood boat with outboard motor[a]	7.5–8.7[a]	Shark gill net
Incidental	Wood boat with inboard motor	17–20	Handline, red grouper longline, and shark longline (10–20 hooks)
Incidental	Fiberglass or wood boat with outboard or inboard motor[a]	7.5–8.7[a]	Handline or fish gill net

[a] Taken from M. J. Saenz et al., Instituto Nacional de Pesca, Centro Regional de Yucalpeten, A.P. 73, Progreso Yucatan, Mexico, unpubl. data.

The great majority of shark fishing activities from Yucatan ports takes place on the Bank of Campeche which is formed by a wide continental shelf (Fig. 8). Sharks are occasionally caught in the deep, oceanic waters of the continental slope.

The fishing units (defined as the complex of a vessel and its set of fishing gear) contributing to the shark fishery of Yucatan were divided into two categories (Table 2). The first are fishing units fishing for sharks as the target species, and consists of two types: small fiberglass ships 10–13 m long with inboard motors, and wood or fiberglass boats with outboard motors that are 7.5–8.7 m long. Both of these units use shark gill nets as the fishing gear. The second category has two kinds of fishing units and includes those vessels targeting other species but often landing sharks as a bycatch. The first of these units are wooden ships 17–20 m in length with inboard motors, which fish for red grouper (*Epinephelus morio*) using handlines and longlines specially designed for this species. Occasionally these fishermen set small longlines for sharks (20 hooks) overnight as a complementary activity. The second type of fishing unit are fiberglass or wood boats 7.5–8.7 m long with outboard motors. These fishermen use handlines for red grouper or gill nets for king mackerel.

For both categories of fishing units, the size of the vessel determines the actual geographical range where they can fish. Size also determines the length of each trip. The small boats make short 1–3 day trips and never going farther than a few kilometers from the coast fishing no deeper than 40–50 m. These vessels fish primarily for coastal species.

The bigger boats in both categories make trips 7–15 days long and occasionally sail to the edge of the continental shelf (250-m depth). These vessels can catch oceanic, deep water, and coastal species.

Kinds of Sharks Fished in Yucatan

To date, 25 species of sharks representing 8 families have been identified by the authors while sampling the commercial catches. The species mix is typical of tropical waters, with carcharhinids (14 species), and sphyrnids (3 species) being the most abundant (Table 3). Catch composition by number sampled indicated there were four primary and four secondary species comprising most of the catch (Fig 9). The primary species were *Rhizoprionodon terraenovae*, *Sphyrna tiburo*, *Mustelus norrisi*, and *Carcharhinus falciformis*, and together they represented 66.1% of the catch. Secondary species were *Carcharhinus leucas*, *C. limbatus*, *C. obscurus*, and *C. plumbeus* with 20.8% of the catches; the remaining 13.1% included another 17 species.

From the total weight data, the most important big sharks were *C. leucas*, *C. obscurus*, and *C. falciformis* which made up 70.5% of this group, with *C. plumbeus* and *Galeocerdo cuvieri* contributing 13.5%. Another twelve species completed the remaining 16%. For small sharks two species (*Mustelus norrisi* and *Rhizoprionodon terraenovae*) accounted for 72.1% of the total weight sampled (Fig. 10). *Sphyrna tiburo* was third with 17.6%, and *C. acronotus* fourth with 9.1% of the small shark group. Another four species comprised the remaining 1.2%.

Analysis of the catch composition has shown that the seven most important species in the Yucatan fishery are *Carcharhinus falciformis*, *C. leucas*, *C. obscurus*, *C. plumbeus*, *Rhizoprionodon terraenovae*, *Mustelus norrisi*, and *Sphyrna tiburo*. Length-weight equations were calculated for these species (Table 4).

Population Structure of the Important Shark Species

A size frequency distribution for female and male silky sharks, *Carcharhinus falciformis*, is shown in Figure 11. For both sexes there were two clearly differentiated clusters. The first and largest of these clusters represents early juveniles and newborn sharks. The respective modal classes for females and males in this group was 90 and 75 cm TL. For both sexes the second cluster comprised mostly adult silky sharks; modal classes in this cluster were 275 and 260 cm TL for females and males respectively. Individuals in the size classes corresponding to late juveniles and preadult stages were infrequently observed, suggesting silky sharks may migrate to more oceanic waters beyond the reach of Yucatan's fishing vessels. The fact that modal lengths for females were larger in both clusters of data (Fig. 11) is

Table 3.
Shark families and species present in Yucatan's fishery.

Family	Species
Hexanchidae	*Hexanchus vitulus*
Squalidae	*Squalus cubensis*
	Squalus blainvillei
Ginglymostomatidae	*Ginglymostoma cirratum*
Lamnidae	*Isurus oxyrinchus*
Alopidae	*Alopias superciliosus*
Carcharhinidae	*Carcharhinus acronotus*
	Carcharhinus altimus
	Carcharhinus brevipinna
	Carcharhinus falciformis
	Carcharhinus leucas
	Carcharhinus limbatus
	Carcharhinus obscurus
	Carcharhinus perezi
	Carcharhinus plumbeus
	Carcharhinus porosus
	Carcharhinus signatus
	Galeocerdo cuvieri
	Negaprion brevirostris
	Rhizoprionodon terraenovae
Triakidae	*Mustelus canis*
	Mustelus norrisi
Sphyrnidae	*Sphyrna lewini*
	Sphyrna mokarran
	Sphyrna tiburo

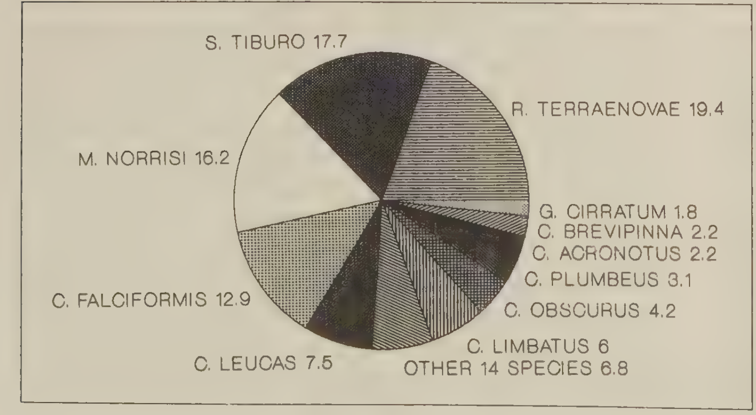

Figure 9.
Species composition of sampled sharks from Yucatan's commercial fishery, shown as percent of number of individuals.

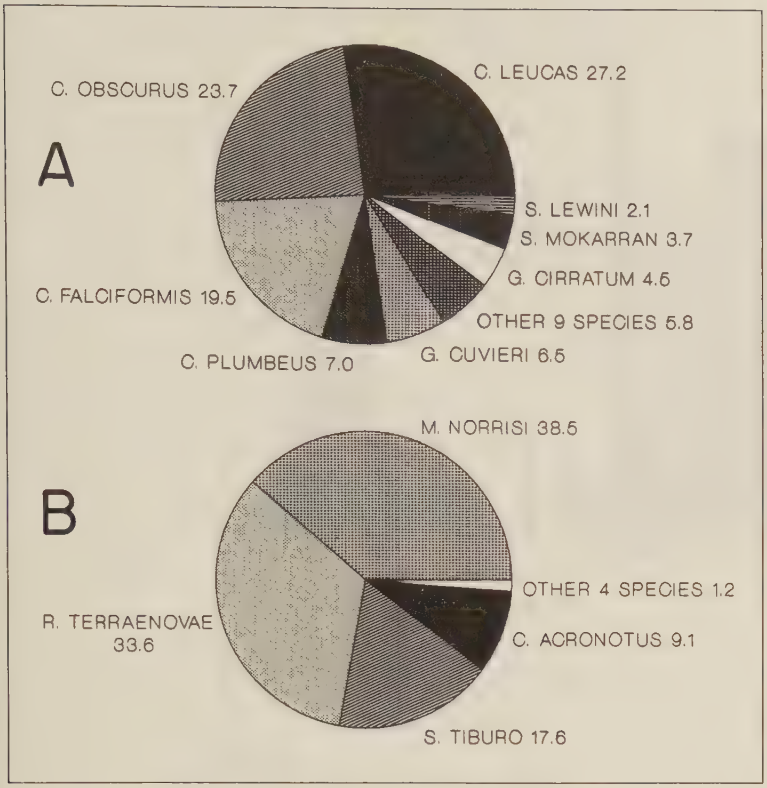

Figure 10.
Species composition of sampled sharks from Yucatan's commercial fishery, shown as percentage of total weight for each species. A, Sharks that grow to more than 1.5 m TL; B, Sharks that do not exceed 1.5 m TL.

Table 4.
Length-weight equations for the 7 most important species from the shark fishery of Yucatan, Mexico. *TW* = total weight; *GW* = gutted weight; *TL* = total length; *n* = sample size; *r* = correlation.

Species	Equation	n	r
Carcharhinus falciformis	$TW = 1.899 \times 10^{-6}\ TL^{3.1915}$	102	0.992
Carcharhinus falciformis	$GW = 1.806 \times 10^{-6}\ TL^{3.1867}$	188	0.9858
Carcharhinus leucas	$TW = 1.1074 \times 10^{-5}\ TL^{2.9234}$	182	0.953
Carcharhinus obscurus	$TW = 4.8459 \times 10^{-6}\ TL^{3.021}$	74	0.939
Carcharhinus plumbeus	$TW = 4.9181 \times 10^{-7}\ TL^{3.4798}$	67	0.975
Rhizoprionodon terraenovae	$TW = 5.6223 \times 10^{-6}\ TL^{2.8973}$	452	0.948
Sphyrna tiburo	$TW = 6.9532 \times 10^{-7}\ TL^{3.3718}$	427	0.961
Mustelus norrisi	$TW = 1.1832 \times 10^{-6}\ TL^{3.1828}$	293	0.931

probably the result of a differential growth rate as well as a larger asymptotic size for females, as observed in other selachians (Schwartz 1983; Pratt and Casey 1983; Casey et al. 1985). The overall sex ratio for this species was 1:1. This, together with the observance of some signs of copulation (claspers bearing edema and subdermal hemorrhage) and the fact that silky sharks are born in Yucatan's waters is evidence of the existance of a mating-nursery area within this zone for *C. falciformis*. The large proportion of juveniles of *C. falciformis* found in the commercial landings is a potential problem, for if the total mortality of juveniles exceeds a limit that prevents minimum recruitment levels of the species, this could have catastrophic effects upon the local silky shark population.

In Yucatan waters, the bull shark, *Carcharhinus leucas*, is represented only by preadult and adult sized sharks (Fig. 12). The modal classes for females and males were 195 and 235 cm TL respectively, although females reached the largest sizes (265 cm TL). According to sizes at maturity given by Castro (1983), most individuals of both sexes found in this area are adults. However, the absence of newborn and early juveniles, the presence of fewer big females,

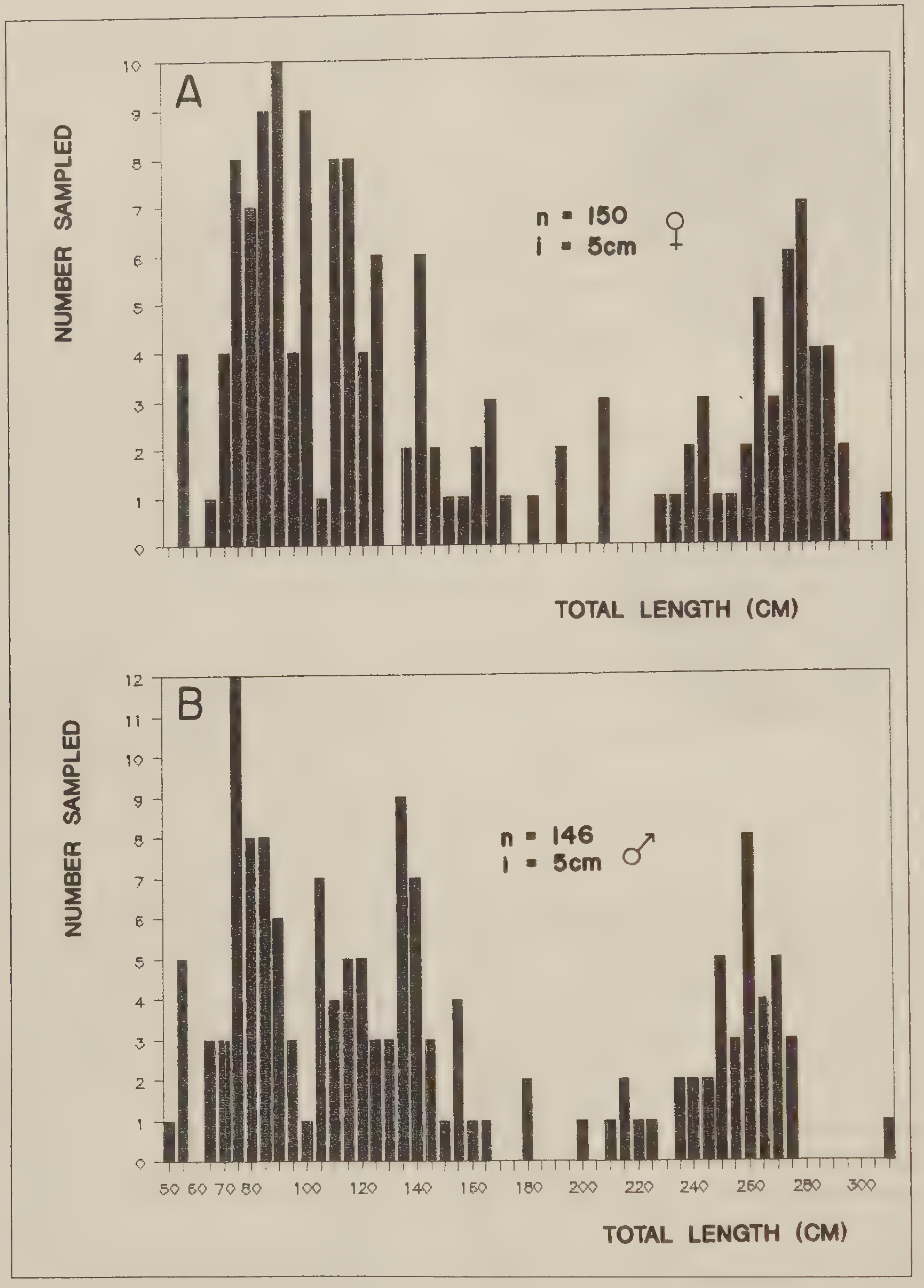

Figure 11.
Length-frequency distribution of *Carcharhinus falciformis* sampled from the commercial fishery of Yucatan, Mexico, between March 1985 and December 1986. A, Females; B, Males; (sex ratio is 1:1); *i* = class interval; *n* = total number of individuals in graph.

plus the strongly male biassed sex ratio (1:2.5) suggests that mating and breeding takes place somewhere outside of the fishing grounds of the Yucatan fishery. Coastal lagoons in the Atlantic coast of the United States seem to be a major breeding and nursery area for the bull shark (Snelson et al. 1984). There are also a few reports of nursery areas in southeast Mexico for this species, particularily in Laguna de Terminos, Campeche and Bahia Chetumal, Quintana Roo (Castro-Aguirre 1978; S. P. Applegate et al., Instituto de Geologia, Universidad Nacional Autonoma de Mexico, A.P. 70-296, Mexico, D.F., 04510 Mexico, unpubl. data). It might be possible that the lack of suitable coastal lagoons make the northern part of the Bank of Campeche only a temporal habitat or feeding ground for this species on their migrations to breeding and mating areas on the nearby coasts of Quintana Roo, Campeche and even Florida.

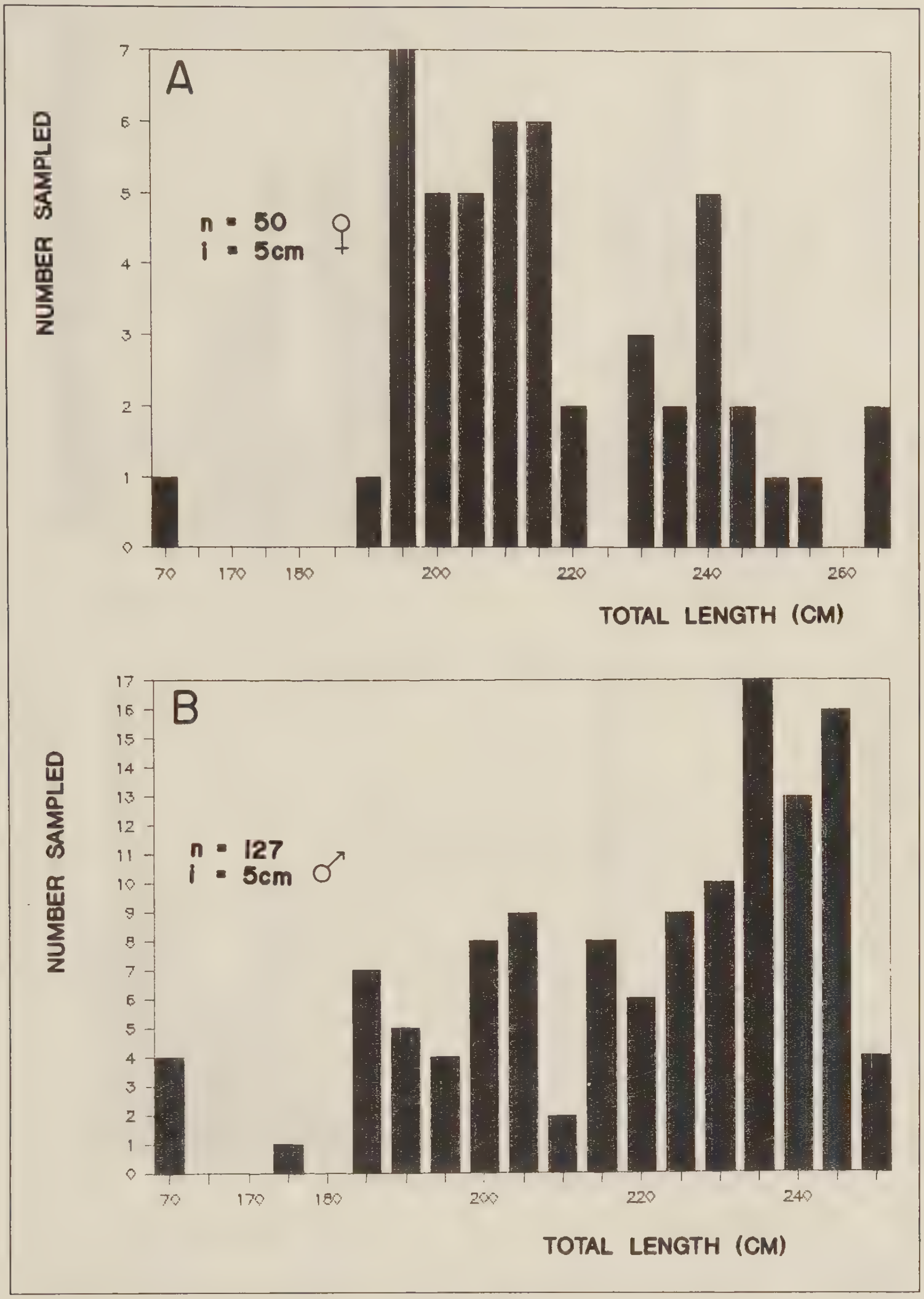

Figure 12.
Length-frequency distribution of *Carcharhinus leucas* sampled from the commercial fishery of Yucatan, Mexico, between March 1985 and December 1986. A, Females; B, Males; (sex ratio is 1:2.5); *i* = class interval; *n* = total number of individuals in graph.

For *Carcharhinus obscurus*, the dusky shark, only preadult and adult sizes were found in the commercial catches, with a few embryos the only early stages present. There were two length modes for females at 325 and 330 cm TL, while males had a single mode at 315 cm TL (Fig. 13). The sex ratio favored males in a proportion of 1:1.7. This population structure suggests dusky sharks do not have breeding or nursery areas on the Bank of Campeche. According to J. A. Musick and J. A. Colvocoresses (Virginia Institute of Marine Science, Gloucester Point, VA 23062, unpubl. data) the primary nursery areas for this species seem to be located along the central Atlantic coast of the United States.

Size frequency distributions for sandbar sharks, *Carcharhinus plumbeus*, were separated into two groups for females and for males (Fig. 14). Adults of both sexes dominated

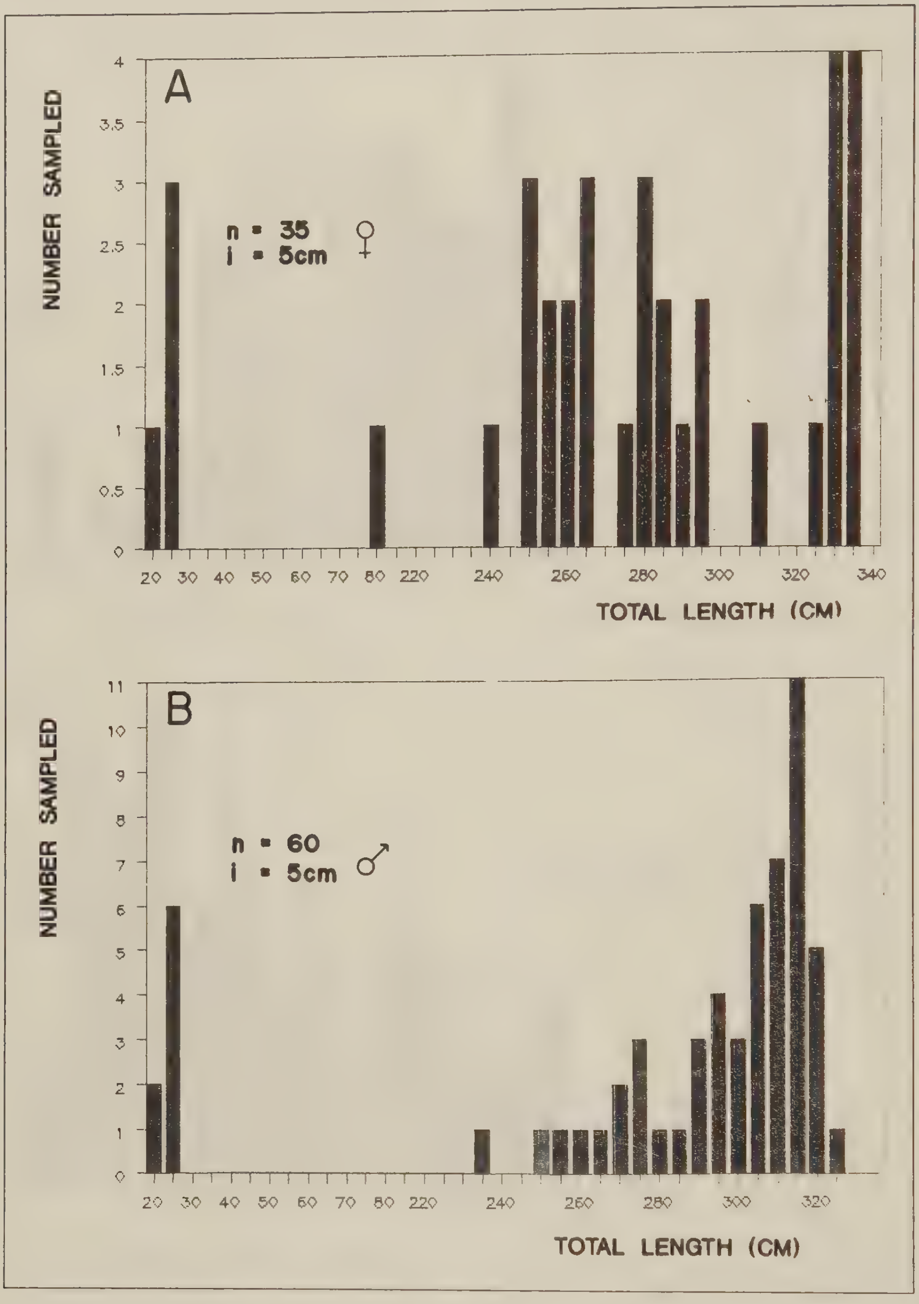

Figure 13.
Length-frequency distribution of *Carcharhinus obscurus* sampled from the commercial fishery of Yucatan, Mexico, between March 1985 and December 1986. A, Females; B, Males; (sex ratio is 1:1.7); *i* = class interval; *n* = total number of individuals in graph.

the catch with sharks in the lower end of the distribution being represented by middle-sized juveniles. No newborns embryos or late juveniles were recorded for this species. The modal size classes were 205 cm TL for females, and 180 and 210 cm TL for males. The sex ratio showed there were 1.2 females per male. Primary nursery areas for this species are located along the eastern coast of the United States and the northern Gulf of Mexico (Springer 1960). None have been located along the Mexican coast, however no intensive search for them has yet been conducted. Analysis of the present population structure suggests that the Bank of Campeche may be serving as a mating site for sandbar sharks.

For the sharpnose shark, *Rhizoprionodon terraenovae*, the population structure for both sexes showed the presence of all developmental stages from newborn to large adult

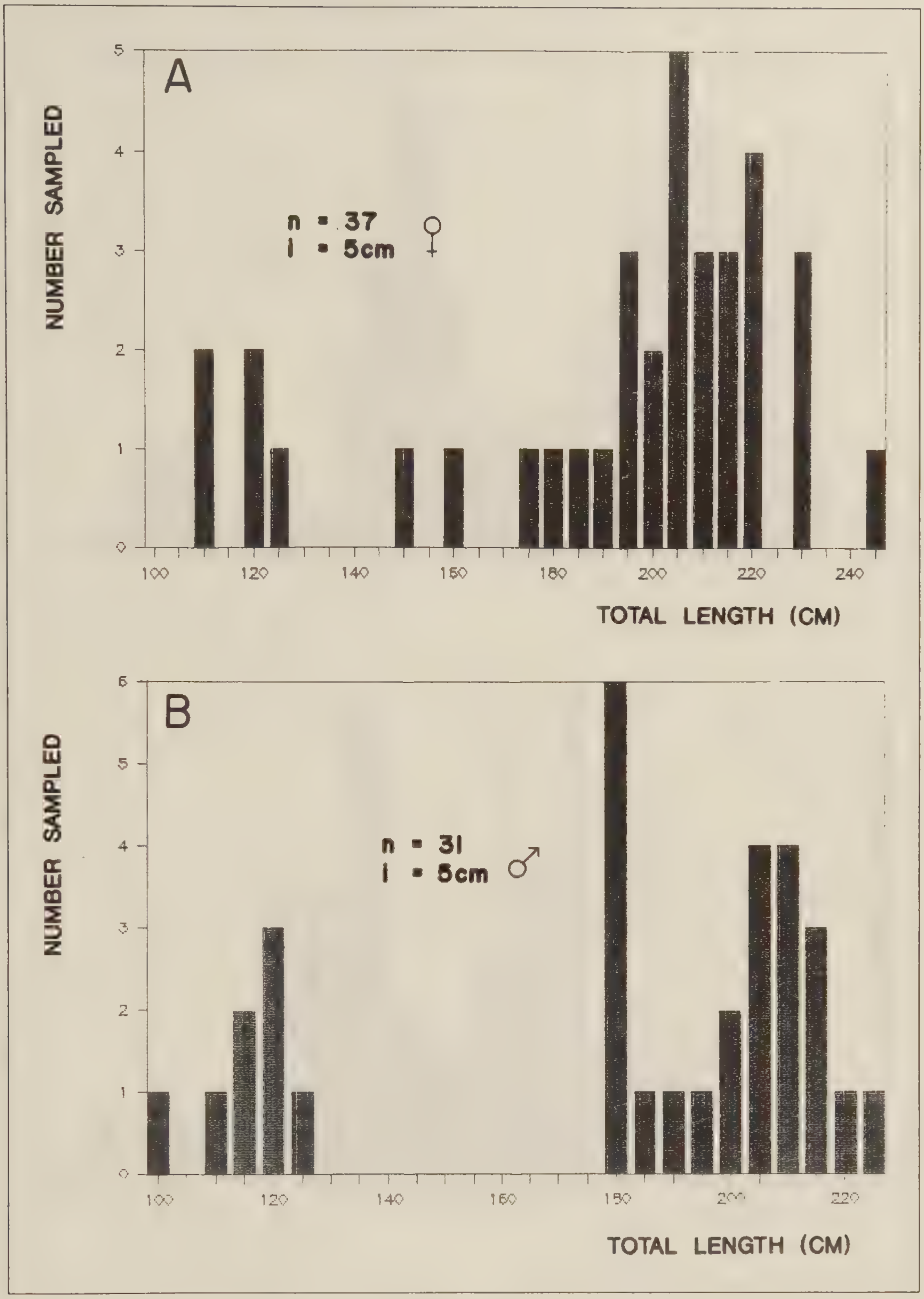

Figure 14.
Length-frequency distribution of *Carcharhinus plumbeus* sampled from the commercial fishery of Yucatan, Mexico, between March 1985 and December 1986. A, Females; B, Males; (sex ratio is 1.2:1); *i* = class interval; *n* = total number of individuals in graph.

sharks in Yucatan's fishing grounds (Fig. 15). The modal classes of both sexes were coincident at 72 cm TL. The sex ratio favored the females slightly at a rate of 1.2:1. From results shown here and data from other studies conducted in the area (Bonfil 1987; C. C. Faustch, Instituto Nacional de Pesca, Centro Regional de Isla Mujeres, A.P. 45, Isla Mujeres, Quintana Roo, Mexico, unpubl. data; M. Seca and D. Murillo, Instituto Nacional de Pesca, Centro Regional de Campeche, Km. 5 Carretera Lerma, Campeche, Campeche, 24000 Mexico, unpubl. data; Uribe, Instituto Nacional de Pesca, Centro Regional de Campeche, Km. 5 Carretera Lerma, Campeche, Campeche, 24000 Mexico, unpubl. data) it is clear that the whole Bank of Campeche supports a major population of sharpnose sharks.

The population structure of the smoothhound shark, *Mustelus norrisi*, is shown in Figure 16. Almost all female

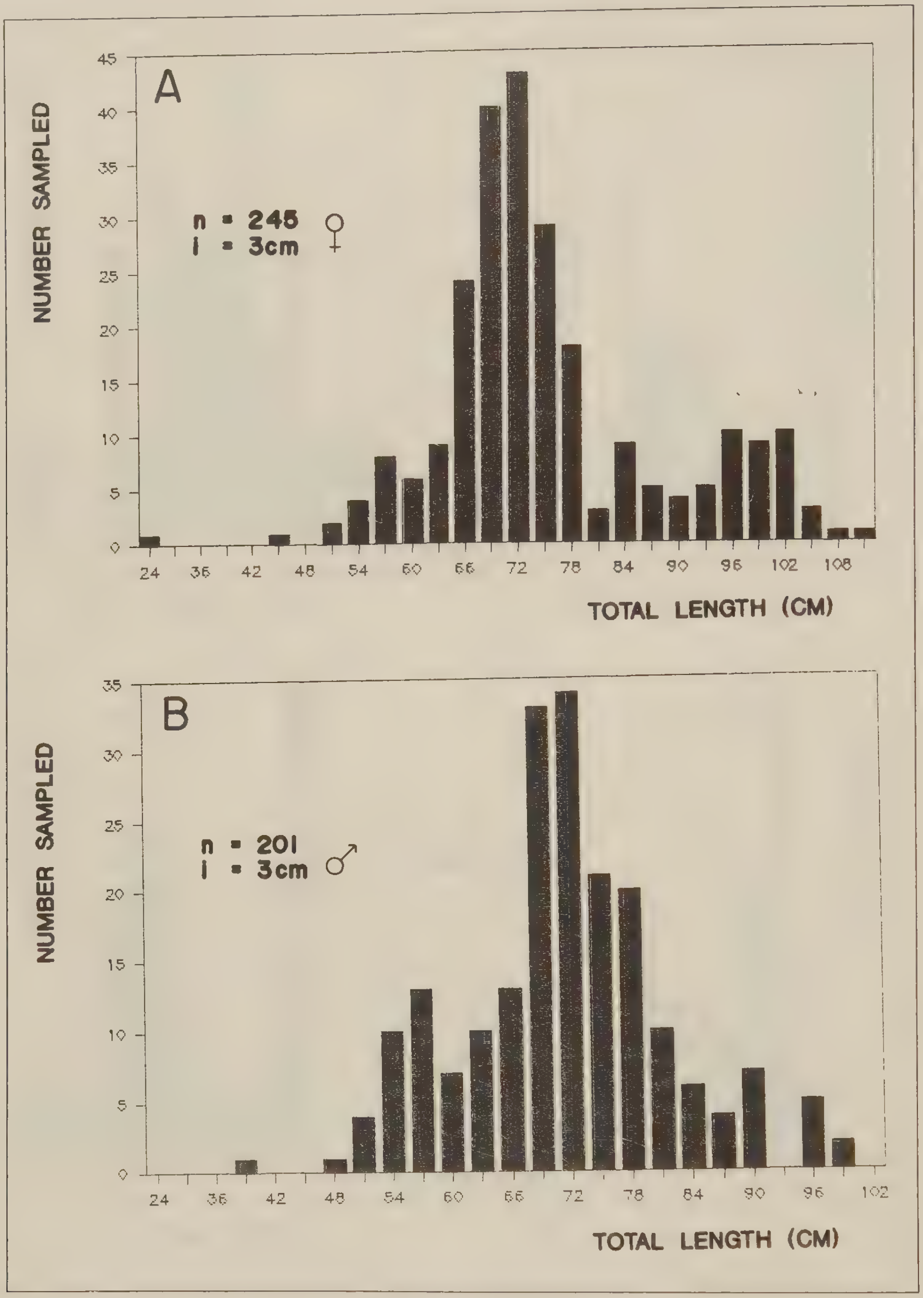

Figure 15.
Length-frequency distribution of *Rhizoprionodon terraenovae* sampled from the commercial fishery of Yucatan, Mexico, between March 1985 and December 1986. A, Females; B, Males; (sex ratio is 1.2:1); *i* = class interval; *n* = total number of individuals in graph.

size classes throughout the length range of the species were represented, with the exception of two size class gaps at 78–80 and 123–125 cm TL, possibly due to sampling size. Modal size was 105 cm TL. Males had a shorter length range than females, but occured at most sizes except between 108 and 117 cm TL. The modal size was 90 cm TL, 15 cm shorter than that of the females. The sex ratio was 1.4:1 for females-males. This deep water species seems to form concentrated populations along the edge of the continental shelf of the Bank of Campeche, because all stages are available to the fishery in that area.

The size frequency distribution for the bonnethead shark, *Sphyrna tiburo*, showed that females attain a much greater size than males, at least in Yucatan's waters (Fig. 17). Both distributions had size class modes at 60 cm TL, possibly due to gear selectivity. The population structure

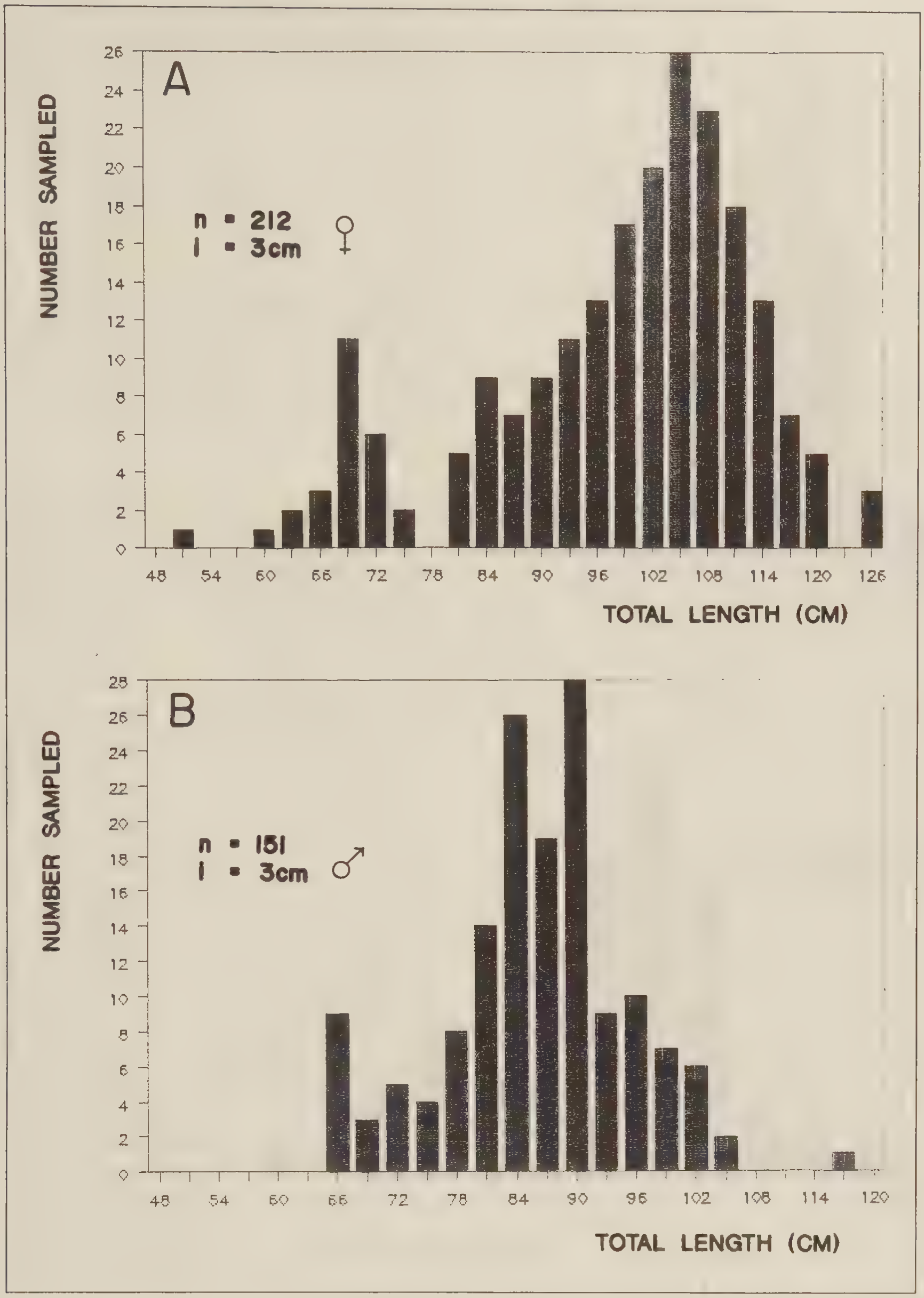

Figure 16.
Length-frequency distribution of *Mustelus norrisi* sampled from the commercial fishery of Yucatan, Mexico, between March 1985 and December 1986. A, Females; B, Males; (sex ratio is 1.4:1); *i* = class interval; *n* = total number of individuals in graph.

of the Yucatan sample included all developmental stages of this species indicating that the life cycle may be completed within the area. The sex ratio was slightly biased toward the males at 1:1.4. The bonnethead shark is another species that together with the sharpnose shark is found abundantly around the entire Yucatan peninsula (M. Seca and D. Murillo, unpubl. data; J. Uribe, unpubl. data).

Recommendations

Even though studies of the shark fishery of Yucatan are far from complete, available information suggests that this fishery could be reaching an equilibrium level, thus, increasing the fishing pressure is not recommended at the present time. This recommendation is based in part on the experiences of other commercial fisheries for sharks else-

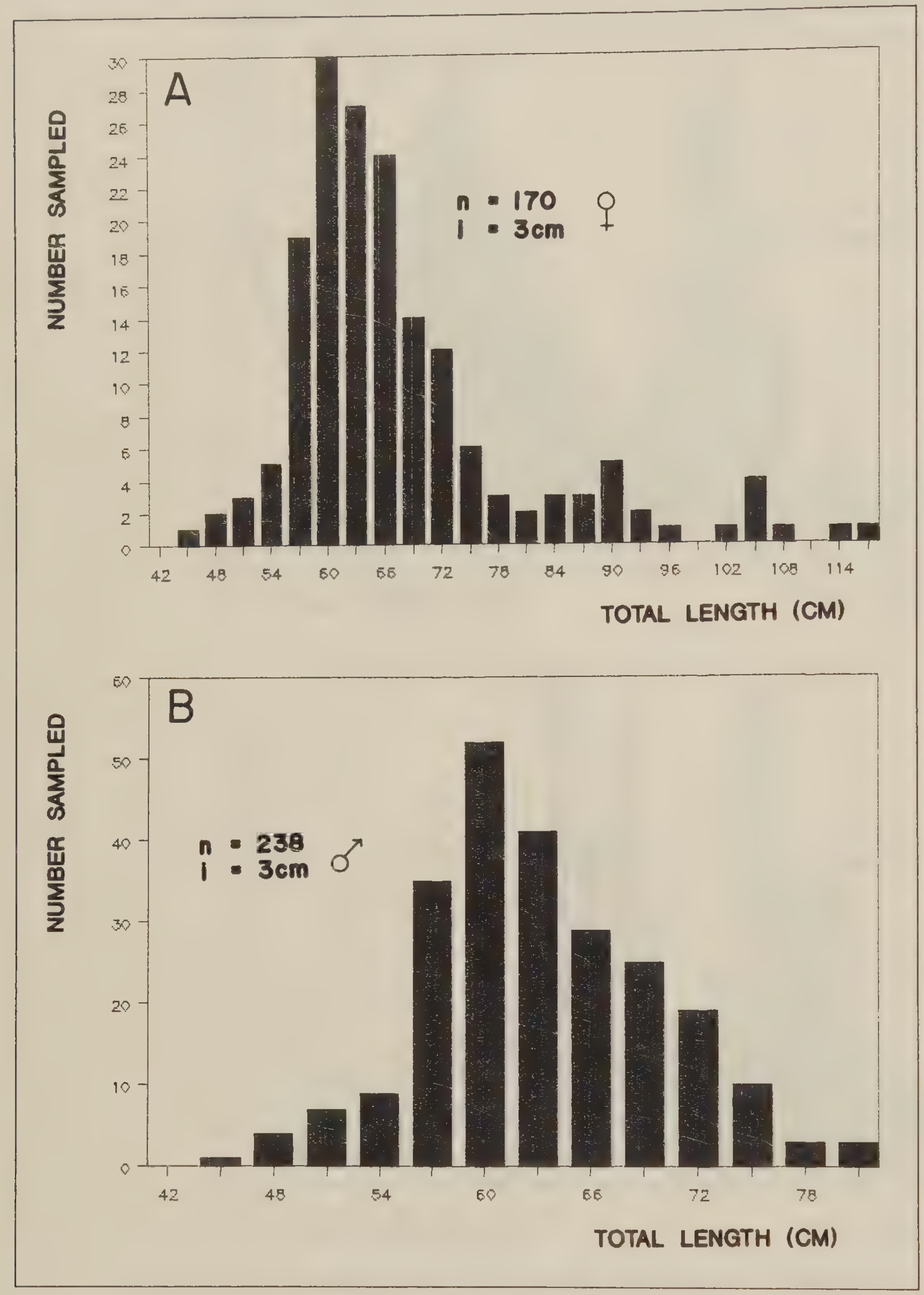

Figure 17.
Length-frequency distribution of *Sphyrna tiburo* sampled from the commercial fishery of Yucatan, Mexico, between March 1985 and December 1986. A, Females; B, Males; (sex ratio is 1:1.4); *i* = class interval; *n* = total number of individuals in graph.

where in the world where large expansions of the fishery have caused rapid depletion of the exploited populations (Holden 1977; Anderson 1990). Further research on size and the dynamics of the principal Mexican populations is needed before any action leading to an increase in fishing effort can be undertaken. For silky shark catches, it would be wise to implant a preventive minimum size to assure incorporation of enough juveniles into the local breeding population.

Future research should cover life cycles of the main species. Expansion of tagging programs in the area would help define the migratory patterns of the sandbar and dusky sharks, and would help to develop basic information about the migrations of silky and bull sharks, which are poorly understood. This studies would need joint efforts with other scientists and institutions both in Mexico and the United States.

Acknowledgments

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Estimates of Large Shark Catches in the Western Atlantic and Gulf of Mexico, 1960–1986

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ABSTRACT

Catches of large sharks (excluding dogfishes) are presented for the period 1960–1986 in the Northwest and western Central Atlantic Ocean and Gulf of Mexico, particularly within the U.S. Fishery Conservation Zone (FCZ), based on reported catch statistics and estimates of unreported bycatch in fisheries directed towards other species. The major sources of catch in the Atlantic FCZ have been the U.S. recreational fishery, followed by the U.S. and Canadian swordfish longline fisheries and the Japanese tuna longline fisheries. The major sources of catch in the Gulf FCZ have been the U.S. recreational, shrimp, groundfish, and snapper–grouper fisheries. Although total catch levels are uncertain, reported commercial catches as well as most of the estimated catches and bycatches have increased in recent years.

Introduction

This paper is an update of an earlier attempt (Anderson 1985) to analyze various sources of catches of large sharks in the Northwest and western Central Atlantic Ocean and Gulf of Mexico. Large or pelagic sharks are defined as all sharks except dogfish (Squalidae). Anderson (1985) attempted to assemble a data base of reported and unreported catches for use by the Mid-Atlantic Fishery Management Council in developing a fishery management plan for sharks in the United States Atlantic Fishery Conservation Zone (FCZ).

Anderson (1985) presented data for 1960–1981. This paper updates the Anderson (1985) paper by revising some of the catch figures from 1978 onwards and by analyzing various time series of catches for 1982–1986. Since the author did not have access to all of the data sources used in preparing the first paper, the updated estimates in this paper are incomplete and, in some cases, based on uncertain assumptions. The results, therefore, must be treated as preliminary and should be used primarily to indicate trends.

Reported Commercial Catch

Northwest Atlantic

Reported commercial catches (defined as the live weight equivalent of landings) of large sharks from the Northwest Atlantic (FAO Area 21) (Fig. 1) for 1960–1986 are given in Table 1 and Figure 2. Data sources for 1960–1981 were described in Anderson (1985). Data for 1982–1986 were obtained from the Northwest Atlantic Fisheries Organization (NAFO) which replaced the International Commission for the Northwest Atlantic Fisheries (ICNAF) in 1979 (Statistical Bulletins 32–34 and NAFO Scientific Council Studies Docs. 86/22 and 87/20).

Aside from the 1960s, when catches reached a high of over 8,400 metric tons (t) as a result of an intensive fishing effort by Norway for porbeagles, *Lamna nasus*, catches have been less than 800 t per year. Reported catches declined every year from 1980 to 1985 before increasing to 564 t in 1986.

United States catches increased in the 1980s relative to the prior 20 years. The average annual catch during 1960–1979 was 65 t, whereas during 1980–1986, it was 165 t (Tables 1 and 2).

Western Central Atlantic and Gulf of Mexico

Reported commercial catches of large sharks from the western Central Atlantic and Gulf of Mexico (FAO Area 31) (Fig. 1) for 1965–1986 are given in Table 3 and Figure 3. Data sources for 1965–1981 were given in Anderson (1985). Data for 1982–1986 were obtained from Volumes 58 and 60 of the FAO Yearbook of Fishery Statistics and (for 1986) from Robinson (Fishery Information, Data and

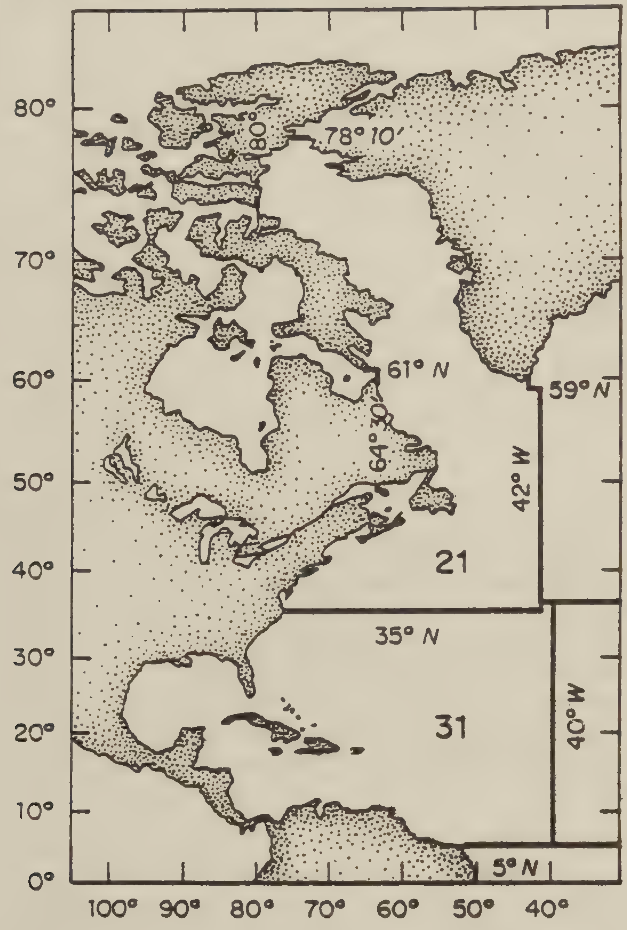

Figure 1.
Map showing FAO Areas 21 and 31 in the Western North Atlantic.

Statistics Service, Fisheries Department, FAO, Rome 00100, Italy, pers. commun., November 1987). Reported U.S. landings for 1978–1986 were obtained from Massey (NMFS, Southeast Fisheries Center, Statistics Division, 75 Virginia Beach Drive, Miami, Florida 33149). Large shark catches from Area 31 are defined as those listed as "requiem sharks" and "various sharks" (beginning with Volume 46 of the yearbook, this latter category was labeled as "sharks, rays, skates, etc.").

The total reported international catches of large sharks from FAO Area 31 steadily increased during 1965–1984, from 4,800 t in 1965 to a high of 26,300 t in 1984, before declining to 21,000 t in 1986. Cuba, Mexico, and Venezuela accounted for most of the catch during this period, averaging 80% of the annual total during 1965–1978 and 92% during 1979–1986. During the last seven years, catches increased at a faster rate than in the previous 14 years (Fig. 3) as a result of significant increases in catches taken by Mexico and to a lesser extent by Venezuela. During 1981–1986, Mexico accounted for an average of 53% of the total catch each year.

Although the reported U.S. catch from Area 31 has been relatively small (Table 3), it increased from a yearly

Table 1.
Reported commercial catch (t) of large sharks by country in the ICNAF/NAFO area (FAO Area 21), 1960–1986.

Year	Canada	Denmark	France	F.R.G.	G.D.R.	Iceland	Japan	Norway	Romania	Spain	U.S.	Others	Total
1960	—	—	—	—	—	—	—	—	—	—	68	—	75
1961	—	—	—	281	—	11	—	1,824	—	—	34	—	2,150
1962	—	—	—	205	—	4	—	2,216	—	—	53	—	2,478
1963	3	—	—	132	—	10	—	5,763	—	—	64	—	5,972
1964	17	54	86	114	—	9	—	8,060	—	—	67	—	8,407
1965	28	1,088	—	154	—	—	—	4,045	—	—	219	—	5,534
1966	80	741	111	53	—	14	—	1,373	—	—	98	3	2,473
1967	51	589	147	—	—	—	36	—	—	—	7	1	831
1968	9	662	—	—	—	1	138	270	—	—	10	27	1,117
1969	7	1,164	—	—	—	1	208	—	—	—	48	—	1,428
1970	5	205	—	—	—	—	674	—	—	—	50	—	934
1971	—	483	—	—	—	1	221	—	40	—	25	—	770
1972	3	260	—	2	16	1	—	87	36	—	46	—	451
1973	—	269	—	—	—	—	—	—	—	—	38	—	307
1974	—	—	—	—	—	—	—	—	105	—	58	—	163
1975	—	80	—	41	—	—	—	—	—	—	110	—	231
1976	—	307	—	11	—	—	3	—	—	1	67	—	389
1977	—	295	—	51	—	—	16	—	—	2	86	4	454
1978	1	121	—	40	—	—	1	—	—	—	91	—	254
1979	3	299	—	—	154	—	23	—	—	1	66	—	546
1980	1	425	—	—	24	—	21	—	—	—	264	—	735
1981	1	344	—	—	16	—	7	—	—	—	184	—	552
1982	3	259	—	—	6	—	14	—	—	—	146	—	428
1983	22	256	—	—	17	—	3	—	—	—	129	—	427
1984	51	126	—	26	19	—	45	17	—	—	132	—	416
1985	51	—	—	—	18	—	3	—	—	—	126	—	198
1986	46	283	—	3	39	—	11	—	—	—	171	11	564

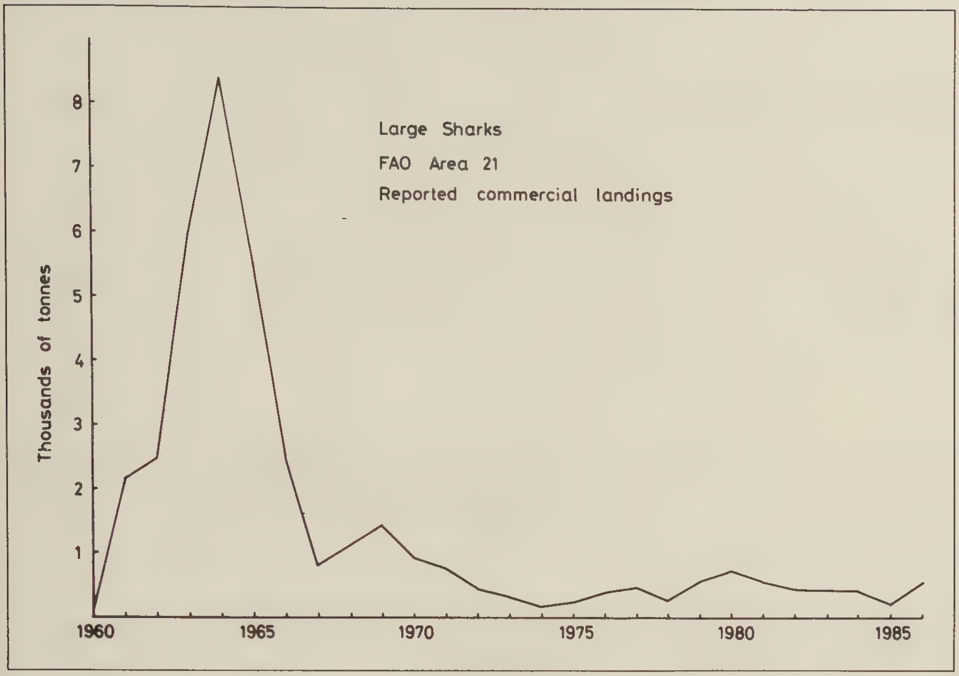

Figure 2.
Reported commercial landings of large sharks in FAO Area 21 (ICNAF/NAFO area), all countries combined, 1960–1986.

Table 2.
Reported United States commercial catch (t) of large sharks by area in the Atlantic Ocean and Gulf of Mexico, 1960–1986.

Year	Nova Scotia–Newfoundland	Maine–Virginia	North Carolina–East Florida	West Florida–Texas	Total
1960	—	68	10	3	81
1961	—	34	11	312	357
1962	—	53	17	4	74
1963	—	64	19	2	85
1964	—	67	15	2	84
1965	—	219	17	1	237
1966	—	98	42	1	141
1967	—	7	598	3	608
1968	—	10	47	2	59
1969	—	48	11	6	65
1970	—	50	5	5	60
1971	—	25	5	8	38
1972	—	46	3	6	55
1973	—	38	16	145	199
1974	—	58	12	11	81
1975	—	110	19	20	149
1976	2	65	34	52	153
1977	—	86	42	76	204
1978	—	91	84	107	282
1979	3	63	50	55	171
1980	7	257	45	170	479
1981	4	180	171	288	643
1982	5	141	186	365	697
1983	10	119	250	396	775
1984	12	120	573	311	1,016
1985	14	112	592	409	1,127
1986	11	160	755	561	1,487

average (geometric mean) of 47 t during 1965–1979 to 1,067 t during 1984–1986. Catches increased every year from 105 t in 1979 to 1,316 t in 1986.

Reported catches by the United States in FAO Areas 21 and 31 combined are given in Table 2 and Figure 4. Catches underwent a marked increase in the last 10–15

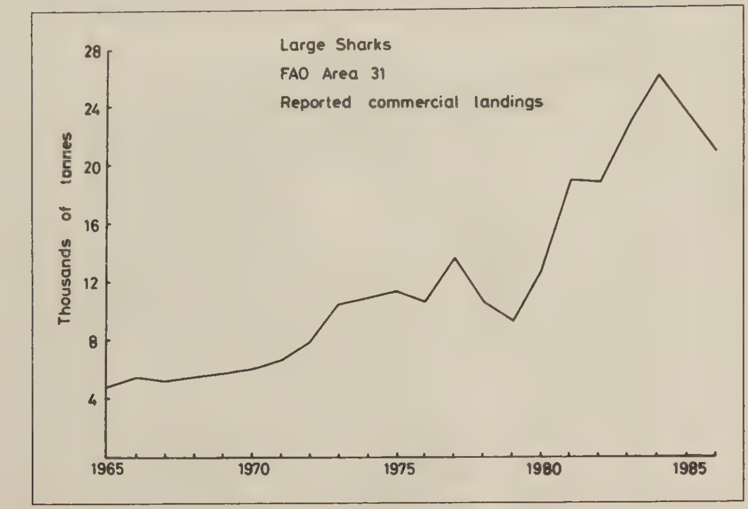

Figure 3.
Reported commercial landings of large sharks in FAO Area 31, all countries combined, 1965–1986.

Table 3.
Reported commercial catch (t) of large sharks in the western Central Atlantic and Gulf of Mexico (FAO Area 31), 1965–1986.

Year	Columbia	Costa Rica	Cuba	French Guiana	Grenada	Japan	Martinique	Mexico	South Korea	Trinidad Tobago	U.S.	Venezuela	Others	Total[a]
1965	—	200	1,300	100	—	800	400	100	—	—	18	1,800	100	4,800
1966	—	200	700	100	—	700	400	200	—	—	43	1,700	1,400	5,400
1967	—	100	1,100	100	—	200	500	200	—	—	601	1,900	100	5,200
1968	—	—	2,700	100	—	100	100	200	—	—	49	2,100	100	5,400
1969	—	—	2,500	100	—	200	100	200	—	—	17	2,400	200	5,700
1970	—	—	2,200	—	—	200	100	1,000	—	200	10	2,200	100	6,000
1971	100	100	2,500	—	—	200	100	1,000	—	300	13	2,300	100	6,700
1972	100	200	2,500	—	—	100	100	1,200	—	300	9	2,400	1,000	7,900
1973	100	—	2,800	—	—	100	100	2,600	—	400	161	3,200	1,000	10,500
1974	100	5	3,100	—	—	74	172	3,189	—	407	23	2,820	1,000	10,900
1975	—	4	3,600	—	—	147	95	3,004	41	375	39	3,064	1,000	11,400
1976	—	3	3,600	—	—	76	193	3,014	74	430	86	2,714	490	10,700
1977	—	2	3,800	—	255	32	140	4,697	28	543	118	3,436	644	13,700
1978	—	3	2,200	—	21	4	154	4,189	11	624	191	2,887	200	10,500
1979	—	5	2,000	—	13	11	181	4,051	—	379	105	2,883	219	9,800
1980	—	5	2,504	—	7	3	181	5,321	—	368	215	4,181	59	12,800
1981	—	9	3,396	—	12	134	181	9,762	17	296	459	4,675	68	19,000
1982	—	8	3,327	—	12	155	212	9,844	8	456	551	4,409	84	19,100
1983	—	21	3,174	—	19	36	197	12,829	258	328	646	5,319	88	22,900
1984	—	12	3,000	—	15	57	200	14,620	866	344	884	6,238	85	26,300
1985	—	7	2,860	—	20	71	178	12,947	531	220	1,001	5,742	74	23,700
1986	—	26	2,860	—	29	71	193	10,454	65	220	1,316	5,742	71	21,000

[a] Rounded to nearest hundred tonnes.

years from 38 t in 1971 to 1,487 t in 1986, with increases occurring in all geographical areas.

Recreational Catch

As indicated in Anderson (1985), the recreational catch of large sharks in the United States is poorly documented, although estimates are based on occasional national and regional angler surveys conducted in 1960, 1965, 1970, 1974–1975, and 1977–1978 and on national surveys conducted annually since 1979. Results of the surveys through 1980 have been presented by Anderson (1985), along with a discussion of potential errors and problems associated with the catch estimates from these surveys. To present a continuous series of recreational catch estimates, Anderson (1985) estimated values for the years lacking surveys by means of interpolation.

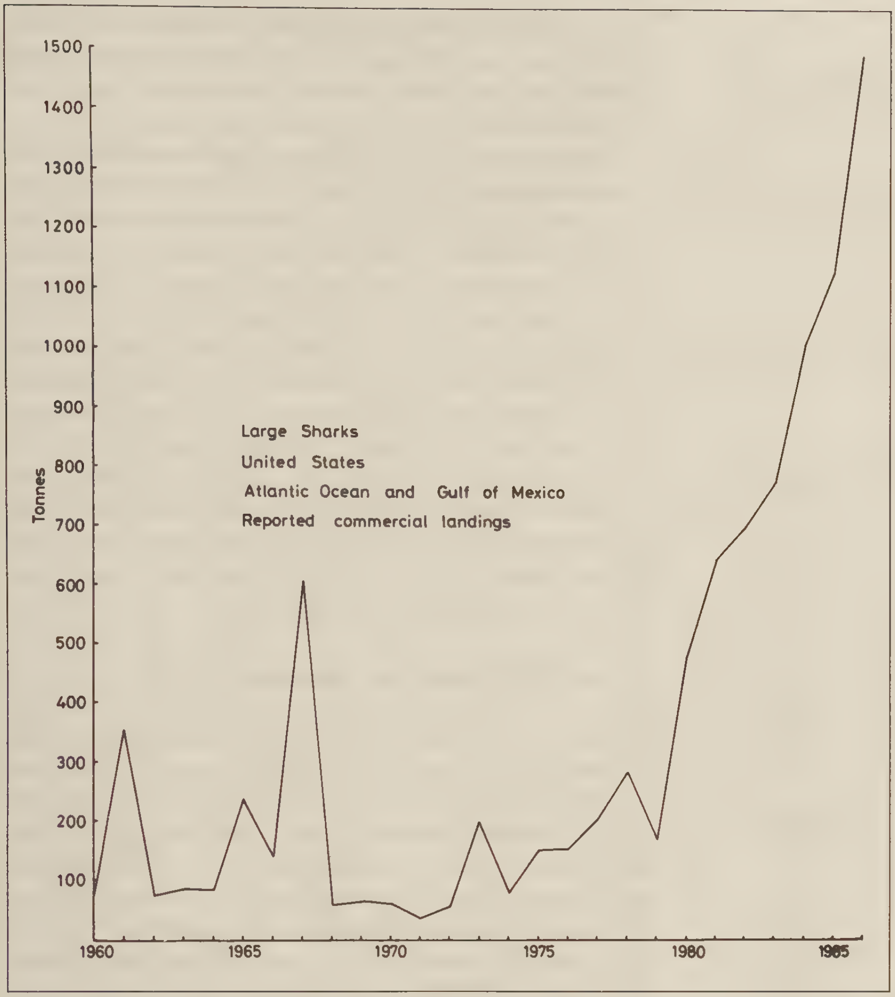

Figure 4.
Reported commercial landings of large sharks in the Atlantic Ocean and Gulf of Mexico by the United States, 1960–1986.

Estimates in this paper are presented for the Atlantic Ocean and Gulf of Mexico by geographical area only for those years in which surveys were conducted during 1965–1986. Estimates for 1979–1980 were revised from those given by Anderson (1985) based on revised data. Data sources for the 1965–1978 estimates were cited by Anderson (1985); the 1979–1986 estimates were obtained from data contained in the U.S. National Marine Fisheries Service Current Fishery Statistics series (Nos. 8322, 8324, 8326, and 8327, and unpublished data).

The total weight of the catch was determined differently for the surveys beginning in 1979 than for those conducted earlier. In the earlier surveys, interviewed anglers provided estimates of the number and average weight of the fish caught, from which an estimated total weight was determined. In the surveys beginning in 1979, catches were estimated in numbers of fish which were 1) available for identification, 2) not available for identification because they had been used for bait, filleted, discarded dead, etc., and 3) not available for identification because they had been released alive. Mean weights were obtained only from fish available for identification (category 1). In Anderson (1985), these mean weights were applied to the number of fish in all three categories in order to obtain an estimate of weight for the total catch. In the present paper, however, the mean weights were applied only to fish in categories 1 and 2. The fish in category 3 were not included in the analysis because they were assumed to have remained alive after their release. Since anglers were not asked to distinguish between fish retained and fish released alive in the pre-1979 surveys, it is uncertain what proportions of the earlier estimates consisted of fish released alive. In addition to the effects of the differences in sampling design and survey methodology among the various surveys, the estimates of catch in weight for 1979–1986 are not equivalent to those for the earlier years because fish discarded alive in the latter period were not included in the data.

The results are shown in Table 4 and Figure 5. There is considerable variation from year to year within each of the geographical areas, and estimates for some areas in some years are extremely high or low. The extreme values (e.g., 29,643 t in 1979 and 617 t in 1980 for Maine–Virginia; 520 t in 1979 and 672 t in 1984 for North Carolina–East Florida; 9,419 t in 1981, 341 t in 1983, and

Table 4.
Estimated U.S. recreational catch (t) of large sharks by area in the Atlantic Ocean and Gulf of Mexico from angler surveys during the period 1965–1986.

Year	Maine–Virginia	North Carolina–East Florida	West Florida–Texas	Total
1965	992	511	1,120	2,623
1966	—	—	—	—
1967	—	—	—	—
1968	—	—	—	—
1969	—	—	—	—
1970	2,753	303	6,798	9,854
1971	—	—	—	—
1972	—	—	—	—
1973	—	—	—	—
1974	2,483[a]	1,798[b]	3,327[b]	7,608
1975	3,186[b]	2,172[a]	2,460[a]	7,818
1976	—	—	—	—
1977	—	—	—	—
1978	5,295	2,532	1,932	9,759
1979	29,643	520	1,177	31,340
1980	617	2,822	1,976	5,415
1981[c]	420	2,686	9,419	12,525
1982	2,148	1,565	1,016	4,729
1983	5,000	2,984	341	8,325
1984	3,563	672	312	4,547
1985	3,621	2,750	2,940	9,311
1986	5,041	1,226	4,165	10,432

[a] Survey estimate included dogfish; large sharks estimated assuming mean of 1965 and 1970 dogfish/large shark ratios.
[b] Interpolated value.
[c] March–December only.

312 t in 1984 for West Florida–Texas) are associated with unusually high or low mean weights relative to those in other years for the areas in question. The exceptionally large estimate of catch in 1979 in the Maine–Virginia area is considered to be particularly invalid because interviewers focused their sampling effort on shark tournaments where trip catch rates were much higher than normal (Anderson 1985). Because of the potential for sampling bias in the all the surveys, the estimates of catch levels must be treated with caution.

There appears to be no obvious trend over time in the catch estimates for the combined Atlantic and Gulf of Mexico areas (Fig. 5). Aside from the exceptionally high (and invalid) estimate for 1979 (31,340 t), estimates have fluctuated about an average of 8,200 t during the period 1970–1986 (excluding 1979), although there was an increase from about 4,500 t in 1984 to about 10,400 t in 1986. In the various geographical areas, year-to-year fluctuations in the estimated catches also occurred. During 1970–1986 (1979 excluded), the Maine–Virginia and West Florida–Texas areas each accounted for an average of 38% of the annual total, while the North Carolina–East Florida area accounted for 24%. Given the uncertainty in these estimates, however, they can be taken only as an approximation of the actual level of catch.

Swordfish Longline Bycatch

Catches of swordfish, *Xiphius gladius*, taken by the United States and Canadian longline fisheries were revised and updated for the period 1978–1986 from data obtained from NAFO Statistical Bulletins and Scientific Council Studies, ICCAT (International Commission for the Conservation of Atlantic Tunas) Statistical Bulletin, Volume 16, and Hoey and Nelson (1988). These catches were used together with bycatch percentages and mean weights of both sharks and swordfish to estimate bycatches of large sharks in these fisheries following the procedure used by Anderson (1985). Mean weights of swordfish caught in the U.S. longline fishery were available by area and year for 1978–1986 from Hoey and Nelson (1988). These weights were also applied to Canadian catches in the respective areas.

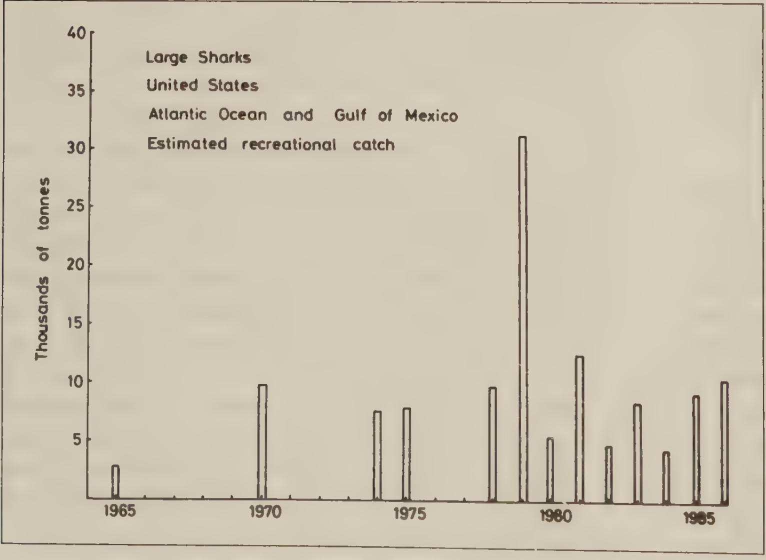

Figure 5.
Estimated U.S. recreational catch (excluding portion released alive) of large sharks in the Atlantic Ocean and Gulf of Mexico, 1965–1986.

The percentages of shark bycatch associated with swordfish catch and mean weights of sharks in the various areas used in this paper are given in Anderson (1985). The bycatch percentages are 234% for Nova Scotia–Newfoundland and Maine–Virginia, 296% for North Carolina–East Florida, and 213% for West Florida–Texas. The mean weights for sharks in each area are 41 kg for Nova Scotia–Newfoundland and Maine–Virginia, 42 kg for North Carolina–East Florida, and 36 kg for West Florida–Texas (Anderson 1985).

The U.S. swordfish fleet moved into the Caribbean Sea in December 1984 and catches increased rapidly from 25 t in that month to 395 t in 1985 and 1,153 t in 1986 (Table 5). The percentages of shark bycatch and the mean weight

Table 5.
Estimated bycatch of large sharks in the United States and Canadian swordfish longline fisheries, 1962–1986.

	Swordfish					Sharks				
	Catch (t)							Est. catch (t)		
Year	U.S.	Canada	Total	Mean round wt. (kg)	Catch (numbers)	Est. catch[a] (numbers)	Mean round wt. (kg)	U.S.	Canada	Total
Nova Scotia–Newfoundland										
1962	4	287	291	120	2,425	5,675	41	3	230	233
1963	101	5,049	5,150	123	41,870	97,976	41	79	3,938	4,017
1964	28	3,861	3,889	106	36,689	85,852	41	25	3,495	3,520
1965	24	1,542	1,566	117	13,385	31,321	41	20	1,264	1,284
1966	13	1,734	1,747	91	19,198	44,923	41	14	1,828	1,842
1967	—	2,693	2,693	75	35,907	84,022	41	—	3,445	3,445
1968	7	2,238	2,245	72	31,181	72,964	41	9	2,983	2,992
1969	—	2,175	2,175	70	31,071	72,706	41	—	2,981	2,981
1970	—	3,145	3,145	53	59,340	138,856	41	—	5,693	5,693
1971	—	—	—	—	—	—	—	—	—	—
1972	—	—	—	—	—	—	—	—	—	—
1973	90	—	90	49	1,837	4,299	41	176	—	176
1974	1,081	2	1,083	61	17,754	41,544	41	1,700	3	1,703
1975	995	13	1,008	75	13,440	31,450	41	1,272	17	1,289
1976	1,185	4	1,189	73	16,288	38,114	41	1,558	5	1,563
1977	1,444	97	1,541	84	18,345	42,927	41	1,649	111	1,760
1978	67	3,053	3,120	68	45,727	107,001	41	94	4,293	4,387
1979	635	2,375	3,010	97	30,932	72,381	41	626	2,342	2,968
1980	508	1,692	2,200	72	30,415	71,171	41	674	2,244	2,918
1981	444	551	995	79	12,619	29,528	41	540	671	1,211
1982	597	938	1,535	62	24,945	58,371	41	931	1,462	2,393
1983	687	952	1,639	64	25,510	59,693	41	1,026	1,421	2,447
1984	931	477	1,408	58	24,110	56,417	41	1,529	784	2,313
1985	1,255	412	1,667	57	29,117	68,134	41	2,103	690	2,793
1986	1,393	781	2,174	52	41,421	96,925	41	2,546	1,428	3,974
Maine–Virginia										
1962	62	68	130	120	1,083	2,534	41	50	54	104
1963	951	2,593	3,544	83	42,699	99,916	41	1,099	2,998	4,097
1964	1,033	3,961	4,994	84	59,452	139,118	41	1,180	4,524	5,704
1965	862	2,403	3,265	74	44,122	103,245	41	1,118	3,115	4,233
1966	486	1,835	2,321	74	31,365	73,394	41	630	2,379	3,009
1967	340	1,852	2,192	65	33,723	78,912	41	502	2,733	3,235
1968	174	2,109	2,283	56	40,768	95,397	41	298	3,613	3,911
1969	93	2,030	2,123	54	39,315	91,997	41	165	3,607	3,772
1970	32	1,552	1,584	36	44,000	102,960	41	85	4,136	4,221
1971	2	—	2	42	48	112	41	5	—	5
1972	41	—	41	42	976	2,284	41	94	—	94
1973	254	14	268	49	5,469	12,797	41	498	27	525
1974	792	—	792	55	14,400	33,696	41	1,382	—	1,382
1975	1,644	7	1,651	61	27,066	63,334	41	2,586	11	2,597
1976	1,968	11	1,979	49	40,388	94,508	41	3,853	22	3,875
1977	4,429	16	4,445	49	90,714	212,271	41	8,672	31	8,703
1978	2,399	—	2,399	72	33,106	77,468	41	3,176	—	3,176
1979	1,181	595	1,776	78	22,656	53,015	41	1,446	728	2,174
1980	1,320	155	1,475	56	26,492	61,991	41	2,275	267	2,542
1981	932	—	932	75	12,433	29,093	41	1,193	—	1,193
1982	1,476	1	1,477	55	26,768	62,637	41	2,566	2	2,568
1983	1,343	5	1,348	59	22,721	53,167	41	2,172	8	2,180
1984	1,356	12	1,368	50	27,506	64,364	41	2,616	23	2,639
1985	838	138	976	45	21,600	50,544	41	1,779	293	2,072
1986	948	212	1,160	34	34,187	79,998	41	2,681	599	3,280

Table 5. (continued)

	Swordfish					Sharks				
	Catch (t)			Mean round wt. (kg)	Catch (numbers)	Est. catch[a] (numbers)	Mean round wt. (kg)	Est. catch (t)		
Year	U.S.	Canada	Total					U.S.	Canada	Total
					North Carolina–East Florida					
1962	—	—	—	—	—	—	—	—	—	—
1963	—	—	—	—	—	—	—	—	—	—
1964	219	—	219	71	3,085	9,132	42	384	—	384
1965	238	—	238	62	3,839	11,363	42	477	—	477
1966	35	—	35	62	565	1,672	42	70	—	70
1967	—	—	—	—	—	—	—	—	—	—
1968	—	—	—	—	—	—	—	—	—	—
1969	—	—	—	—	—	—	—	—	—	—
1970	—	—	—	—	—	—	—	—	—	—
1971	—	—	—	—	—	—	—	—	—	—
1972	—	—	—	—	—	—	—	—	—	—
1973	—	—	—	—	—	—	—	—	—	—
1974	—	—	—	—	—	—	—	—	—	—
1975	—	—	—	—	—	—	—	—	—	—
1976	263	—	263	42	6,262	18,536	42	779	—	779
1977	275	—	275	39	7,051	20,871	42	877	—	877
1978	527	—	527	55	9,659	28,591	42	1,201	—	1,201
1979	1,818	—	1,818	53	34,139	101,051	42	4,244	—	4,244
1980	2,325	—	2,325	53	43,593	129,035	42	5,419	—	5,419
1981	2,021	—	2,021	53	37,891	112,157	42	4,711	—	4,711
1982	2,211	—	2,211	52	42,523	125,868	42	5,286	—	5,286
1983	2,071	—	2,071	48	43,503	128,769	42	5,408	—	5,408
1984	1,737	—	1,737	42	41,809	123,755	42	5,198	—	5,198
1985	1,500	—	1,500	41	37,006	109,538	42	4,601	—	4,601
1986	903	—	903	37	24,406	72,242	42	3,034	—	3,034
					West Florida–Texas					
1962	—	—	—	—	—	—	—	—	—	—
1963	—	—	—	—	—	—	—	—	—	—
1964	—	—	—	—	—	—	—	—	—	—
1965	—	—	—	—	—	—	—	—	—	—
1966	—	—	—	—	—	—	—	—	—	—
1967	—	—	—	—	—	—	—	—	—	—
1968	—	—	—	—	—	—	—	—	—	—
1969	1	—	1	48	21	45	36	2	—	2
1970	156	—	156	48	3,250	6,923	36	249	—	249
1971	—	—	—	—	—	—	—	—	—	—
1972	—	—	—	—	—	—	—	—	—	—
1973	10	—	10	36	278	592	36	21	—	21
1974	68	—	68	36	1,889	4,024	36	145	—	145
1975	108	—	108	41	2,634	5,610	36	202	—	202
1976	360	—	360	47	7,660	16,316	36	587	—	587
1977	5	—	5	36	139	296	36	11	—	11
1978	26	—	26	54	485	1,033	36	37	—	37
1979	253	—	253	46	5,453	11,615	36	418	—	418
1980	862	—	862	35	24,300	51,759	36	1,863	—	1,863
1981	589	—	589	39	15,184	32,342	36	1,164	—	1,164
1982	628	—	628	45	13,861	29,524	36	1,063	—	1,063
1983	367	—	367	31	11,699	24,919	36	897	—	897
1984	367	—	367	29	12,652	26,950	36	970	—	970
1985	575	—	575	35	16,238	34,587	36	1,245	—	1,245
1986	422	—	422	30	14,227	30,304	36	1,091	—	1,091
					Caribbean					
1984	25	—	25	57	448	955	36	34	—	34
1985	395	—	395	59	6,718	14,308	36	515	—	515
1986	1,153	—	1,153	47	24,337	51,839	36	1,866	—	1,866

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[a] Assuming a shark bycatch in all years of 234% of the swordfish catch in the Nova Scotia–Newfoundland and Maine–Virginia areas, 296% in the North Carolina–East Florida area, and 213% in the West Florida–Texas and Caribbean areas.

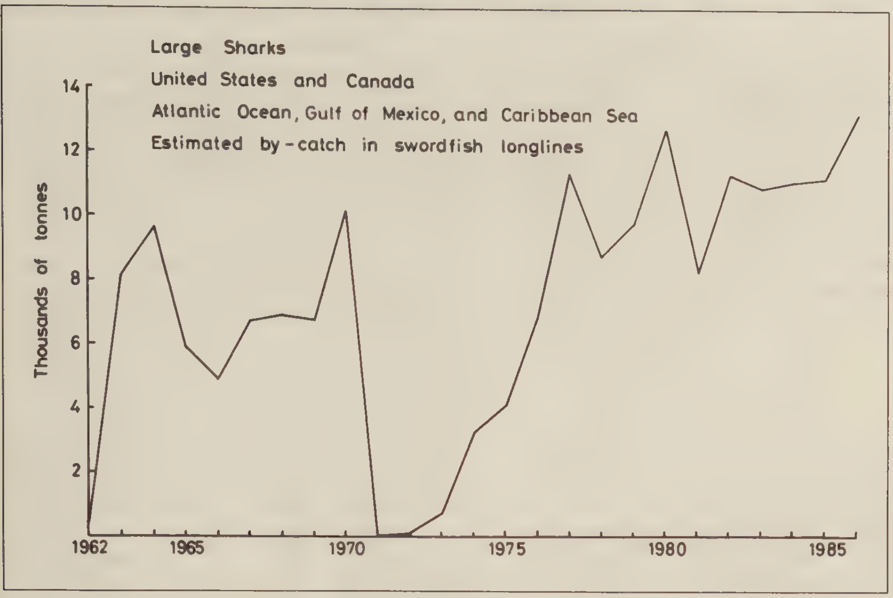

Figure 6.
Estimated bycatch of large sharks in U.S. and Canadian swordfish longline fisheries in the Atlantic Ocean, Gulf of Mexico, and Caribbean Sea, 1962–1986.

for sharks in this area in 1984–1986 were assumed to be the same as in the West Florida–Texas area.

The level of swordfish catches in the U.S. and Canadian longline fisheries during 1981–1986 averaged about 5,300 t per year compared to 6,500 t per year during 1977–1980 (Table 5). In spite of the decline in swordfish catch in weight, the catch in numbers increased as a result of a decrease in the average mean weight of the swordfish (all areas combined) from 79 kg in 1979 to 43 kg in 1986. Consequently, the estimated bycatch of sharks also increased, as the bycatch percentages relate to numbers caught both for swordfish and sharks. The total estimated bycatch of sharks in the Atlantic, Gulf of Mexico, and Caribbean areas reached a high of 13,245 t in 1986 (Fig. 6). During 1981–1984, about 50% of the total shark bycatch occurred each year in North Carolina–East Florida.

An uncertainty associated with the bycatch of sharks in the swordfish longline fisheries is the survival rate of those that are discarded at sea. Data on the survivability of discarded sharks are incomplete, although it may be relatively high for some species (e.g., 70% or higher for blue sharks [Anderson and Teshima 1990]). Therefore, the estimates of bycatch given in Table 5 should not be viewed as necessarily representing estimates of sharks killed.

It should also be noted that some of the sharks taken as bycatch in the U.S. and Canadian swordfish longline fisheries are retained, landed, and probably included in the reported landing statistics (Tables 1–3).

Distant-Water-Fleet Squid Trawl Bycatch

Anderson (1985) documented the bycatch of sharks, as well as other large pelagic fish species, in the distant-water-fleet (DWF) trawl fishery for squid, *Lologo pealei* and *Illex illecebrosus*, in U.S. waters of the Northwest Atlantic (ICNAF/NAFO Subareas 5 and 6) in 1978 and used the 1978 squid/shark bycatch ratio to estimate shark bycatches for other years during 1965–1981. In this paper, that ratio was also applied to the DWF catches of squid during 1982–1986 to estimate the possible bycatch of sharks.

The DWF catch of squid in U.S. waters declined markedly from 37,300 t in 1980 to only 4,500 t in 1986 in response to greatly reduced total allowable levels of foreign fishing (TALFF). Consequently, the estimated shark bycatch declined from 180 t in 1980 to only 22 t in 1986 (Table 6).

Japanese Tuna Longline Bycatch

Anderson (1985) estimated shark bycatches in the Japanese longline fishery for tuna during 1960–1982 using bycatch rates reported by Witzell (1985) for 1978–1982 and effort data (numbers of hooks fished) reported to ICCAT by 5° Marsden squares for the Japanese longline fishery. Estimates were made for the U.S. FCZ in both the Atlantic and Gulf of Mexico (Table 7). The total for both areas combined averaged about 1,150 t annually during 1965–1982, but catches were much higher in the Atlantic than in the Gulf of Mexico. The estimated bycatch for both areas reached a high of 3,261 t in 1981, but dropped markedly to only 523 t in 1982 (all in the Atlantic).

Since the author did not have access to any Japanese catch-effort data for years after 1982, it was impossible to update this time series of shark bycatch estimates.

Other Sources of Bycatch

The only other source of bycatch of large sharks mentioned by Anderson (1985), which is repeated in this paper for 1982–1986, is the bycatch in the Gulf of Mexico in the U.S. trawl fisheries for shrimp and groundfish and the snapper-grouper fishery which was assumed by the Gulf of Mexico Fishery Management Council to exceed, annually, 5 million lb (2,270 t) and 250,000 lb (113 t), respectively, for a total of 2,383 t (Table 7).

Table 6.
Estimated bycatch (t) of large sharks in the distant-water-fleet squid trawl fishery in the U.S. Fishery Conservation Zone in the Northwest Atlantic (ICNAF/NAFO Subareas 5 and 6), 1965–1986. The 1965–1977 and 1979–1986 estimates of bycatch were calculated using the 1978 squid/shark bycatch ratio.

Year	Squid catch	Estimated shark bycatch
1965	176	1
1966	389	2
1967	833	4
1968	4,917	24
1969	8,463	41
1970	18,824	91
1971	21,028	101
1972	47,500	229
1973	55,133	266
1974	53,106	256
1975	49,972	241
1976	46,389	223
1977	39,628	191
1978	26,576	128
1979	29,172	141
1980	37,279	180
1981	34,304	165
1982	28,544	137
1983	13,638	66
1984	11,604	56
1985	7,577	36
1986	4,533	22

Discussion

Reported commercial catches of large sharks in the Western Atlantic and Gulf of Mexico, as well as estimates of recreational catches and bycatches from several fisheries within the overall area, are presented in this paper. It must be stressed, however, that all estimates are subject to considerable error and must be interpreted with caution.

Estimated total large shark catches in the Atlantic FCZ exhibited a general increase from 1965–1985 (Table 7, Fig. 7). Through 1971, other countries accounted for nearly 60% of the annual total, because of a relatively high bycatch in the Canadian swordfish longline fishery and Norwegian catches of porbeagles. Since then, the United States has accounted for a high proportion of the catch. The unusually high estimated catch in 1979 (35,969 t = U.S., 38,185 t = total) was due to the U.S. recreational catch estimate in that year of 30,163 t, which, as explained earlier, is considered to be invalid. Most of the estimated catch since the mid-1970s has been from the U.S. recreational and the U.S. swordfish longline fisheries. The high levels in the longline fishery are contingent upon the continued assumption of high bycatch rates. However, because of a recent diversification by the U.S. longline fleet for large pelagic species, recent bycatch rates of sharks will likely

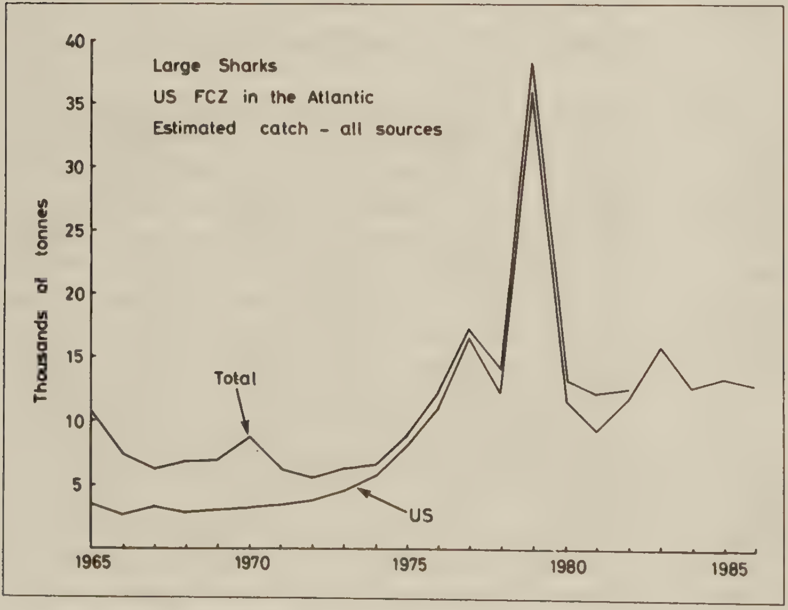

Figure 7.
Estimated catch (total and U.S.) of large sharks in the U.S. Fishery Conservation Zone in the Atlantic Ocean, 1965–1986.

Table 7.
Estimated total catch (t) of large sharks in the U.S. Fishery Conservation Zone in the Atlantic Ocean and Gulf of Mexico by fishery and country (U.S. and others), 1965-1986.

	Commercial		Recreational	Swordfish		Squid	Tuna	All fisheries		
Year	U.S.	Others	U.S.	U.S.	Others	Others	Others	U.S.	Others	Total
Atlantic										
1965	236	2,958	1,503	1,595	3,115	1	1,097	3,334	7,170	10,504
1966	140	1,452	1,813	700	2,379	2	954	2,653	4,787	7,440
1967	605	86	2,125	502	2,733	4	165	3,232	2,988	6,220
1968	57	349	2,435	298	3,613	24	113	2,790	4,099	6,889
1969	59	216	2,746	165	3,607	41	92	2,970	3,956	6,926
1970	55	679	3,056	85	4,136	91	578	3,196	5,484	8,680
1971	30	206	3,363	5	—	101	2,513	3,398	2,820	6,218
1972	49	344	3,669	94	—	229	1,138	3,812	1,711	5,523
1973	54	16	3,975	498	27	266	1,408	4,527	1,717	6,244
1974	70	119	4,281	1,382	—	256	723	5,733	1,098	6,831
1975	129	77	5,358	2,586	11	241	501	8,073	830	8,903
1976	99	31	6,181	4,632	22	223	1,024	10,912	1,300	12,212
1977	128	26	7,004	9,549	31	191	328	16,681	576	17,257
1978	175	1	7,827	4,377	—	128	1,594	12,379	1,723	14,102
1979	116	24	30,163	5,690	728	141	1,323	35,969	2,216	38,185
1980	309	22	3,439	7,694	267	180	1,230	11,442	1,699	13,141
1981	355	13	3,106	5,904	—	165	2,642	9,365	2,820	12,185
1982	332	59	3,713	7,852	2	137	523	11,897	721	12,618
1983	379	13	7,984	7,580	8	66	—	15,943	—	—
1984	705	8	4,235	7,814	23	56	—	12,754	—	—
1985	718	14	6,371	6,380	293	36	—	13,469	—	—
1986	926	58	6,267	5,715	599	22	—	12,908	—	—
Gulf of Mexico										
1965	1	4	1,120	—	—	34	2,383	3,504	38	3,542
1966	1	—	2,255	—	—	—	2,383	4,639	—	4,639
1967	3	1	3,391	—	—	10	2,383	5,777	11	5,788
1968	2	1	4,527	—	—	10	2,383	6,912	11	6,923
1969	6	1	5,663	2	—	4	2,383	8,054	5	8,059
1970	5	4	6,798	249	—	40	2,383	9,435	44	9,479
1971	8	8	5,931	—	—	106	2,383	8,322	114	8,436
1972	6	137	5,063	—	—	96	2,383	7,452	233	7,685
1973	145	435	4,195	21	—	66	2,383	6,744	501	7,245
1974	11	624	3,327	145	—	71	2,383	5,866	695	6,561
1975	20	907	2,460	202	—	212	2,383	5,065	1,119	6,184
1976	52	1,051	2,284	587	—	419	2,383	5,306	1,470	6,776
1977	76	28	2,108	11	—	442	2,383	4,578	470	5,048
1978	107	4	1,932	37	—	196	2,383	4,459	200	4,659
1979	55	6	1,177	418	—	253	2,383	4,033	259	4,292
1980	170	1	1,976	1,863	—	142	2,383	6,392	143	6,535
1981	288	36	9,419	1,164	—	619	2,383	13,254	655	13,909
1982	365	—	1,016	1,063	—	—	2,383	4,827	—	—
1983	396	—	341	897	—	—	2,383	4,017	—	—
1984	311	—	312	970	—	—	2,383	3,976	—	—
1985	409	—	2,940	1,245	—	—	2,383	6,977	—	—
1986	561	—	4,165	1,091	—	—	2,383	8,200	—	—

exhibit greater variability by time and area than those in earlier years, and will need to be estimated accordingly.

Estimated shark catches in the Gulf of Mexico FCZ exhibited some fluctuations during 1965–1986 (Table 7, Fig. 8) that very likely do not reflect actual events, particularly in the U.S. recreational fishery. The estimates of recreational catch in 1970 (6,798 t) (and the extrapolated values between 1965 and 1974) and in 1981 (9,419 t) are excessive, inconsistent with trends in commercial catches, and probably erroneous. The only trend that is consistent among several of the sources of catch and bycatch is an increase in the last few years.

In spite of the uncertainty associated with the estimates of catch of large sharks presented in this paper, there is some consistency in the general increasing trend observed for many of the time series. Catches from commercial fisheries have clearly undergone a pronounced increase in the Gulf of Mexico and other parts of FAO Area 31, although the international total has declined 20% from 1984 to 1986. The increasing trend is evident in both the

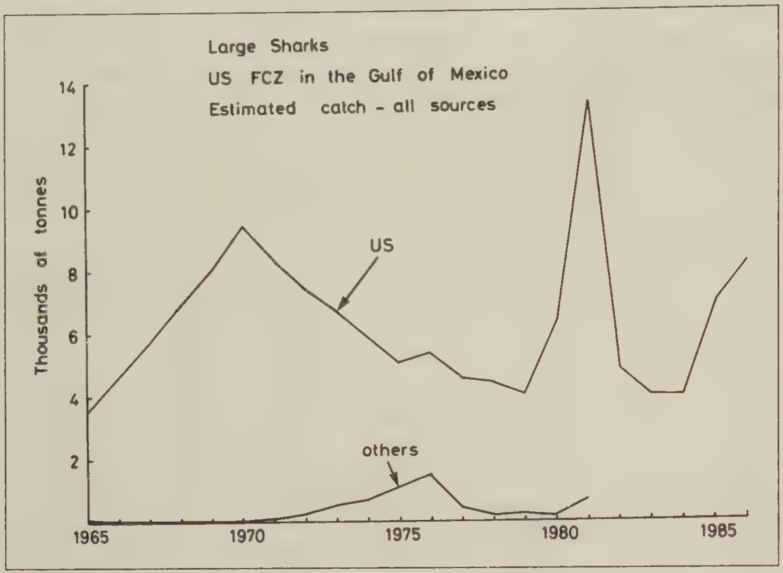

Figure 8.
Estimated catch (U.S. and others) of large sharks in the U.S. Fishery Conservation Zone in the Gulf of Mexico, 1965–1986.

international total and in the U.S. catch, even though the latter has accounted for only 2–3% of the total in the 1980s. Recreational estimates are uncertain, but appear to have increased since the early 1980s for the Atlantic and Gulf of Mexico as a whole. Estimates of bycatch in the swordfish longline fisheries for the Atlantic and Gulf of Mexico have also shown a steady increase since the early 1970s commensurate with the increase in the longline fishery for swordfish.

Attempts should be made to improve the reliability of the various estimates of catch and bycatch presented in this paper. These improvements will require better reporting of bycatches by fishermen and more intensive sampling of the longline and recreational fisheries to obtain data on effort, bycatch, and mean weights. In addition, survival rates of released sharks need to be determined and applied to discard estimates in order to obtain more refined estimates of the true level of sharks that suffer mortality from fishing activities.

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Western North Atlantic Shark-Fishery Management Problems and Informational Requirements[1]

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ABSTRACT

The Mid-Atlantic Fishery Management Council (Council) has primary responsibility for the development of the Western North Atlantic Shark Fishery Management Plan (FMP). Currently, there is a consensus among the five East Coast Councils that an FMP for sharks should be prepared. The current concerns focus on many of the same issues that were germane a decade ago when a shark FMP was initiated and then halted mainly because of inadequate information. These issues include 1) an expanded, nondiscriminant, commercial longline fishery; (2) an existing and rapidly expanding recreational fishery; (3) concern for the extensive waste which occurs from both recreational and commercial activities (especially the rapidly increasing issue of harvesting sharks for the use of only fins); (4) the reproductive strategy (few offspring, late maturation, and slow growth rates) of many species; and (5) realization that increased fishing pressure on specific shark species generally results in overfishing. Essential information for stock assessment is lacking for sharks and thus management is severely handicapped. Critical data needs include: valid growth information, stock delineation, documentation of the catch by species, samples of the population size structure, mortality estimates, independent indices of population abundance through time, and documentation of all (U.S. and other nationals) user groups both recreational and commercial. Data are particularly sparse for foreign fisheries which have expanded outside U.S. controlled waters, and which could be harvesting the same stocks of sharks.

Management Structure

The 1976 Magnuson Fishery Conservation and Management Act (MFCMA) provides for the conservation and management of fishery resources of the United States by establishing an exclusive economic zone (EEZ) of 200 nautical miles. Within the EEZ, the United States has exclusive management authority over all fishery resources except tunas. The Act also established eight Regional Fishery Management Councils whose purpose was to prepare, monitor, and revise fishery management plans. The Mid-Atlantic Fishery Management Council (MAFMC) has primary responsibility for the development of the Western North Atlantic Shark Fishery Management Plan (FMP), with the aid of the other four east coast fishery management Councils.

Shortly after enactment of the MFCMA in 1976, the National Marine Fisheries Service (NMFS) developed an Atlantic Billfishes and Sharks Preliminary Management Plan (PMP), which was rapidly followed by developmental work on an FMP by the Councils. An Inter-Council Shark FMP Committee was created, whose members held several meetings from the initiation of work to the summer of 1980, when they agreed to postpone additional work on an FMP pending completion of an amendment to the PMP. Additionally, other priorities for the Councils and the dearth of information essential for fishery management greatly contributed to the cessation of work on the Shark FMP. No further action was taken until the early 1980s when Cuba applied to fish for sharks in the Gulf of Mexico. Concerns about an expected large bycatch of snappers and groupers in the proposed fishery prompted the Gulf of Mexico Council to draft an FMP for the Gulf of Mexico only. However, prior to submittal of the FMP to the Secretary of Commerce, Cuba withdrew its application.

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[1] VIMS contribution number 1498.

The existing knowledge and information available at the time of the PMP was limited (R. Stone, NOAA, Silver Spring MD 20910, February 1986) and data for all shark species were pooled. The major purpose of the PMP was to control the foreign catch and, as a result, the PMP had fairly stringent restrictions which resulted in few requests for Total Allowable Levels of Foreign Fishing (TALFF). It has been very difficult to develop a foreign directed fishery under the conditions of the PMP. It is believed (J. Casey, NOAA, Narragansett RI 02882, February 1986) that the PMP has successfully decreased the mortality of many shark species.

Despite the apparent effectiveness of the PMP in controlling mortality associated with foreign fishing activities, continuing concerns over increases in the reported commercial catches and the expansion and magnitude of the recreational fisheries, have combined to renew interest in the management of sharks by all five east coast Councils. Another Inter-Council Shark Committee was formed in 1985 with representation from all five Councils. The responsibility of the Committee was limited to assembling and reviewing information and preparing a final recommendation for the Councils concerning whether or not to proceed with the development of an FMP (McHugh 1985). It was under the direction of this Committee that a panel of experts was convened in 1986.

Current Issues

Currently, there is a consensus among a number of members of the five east coast Councils that an FMP for sharks should be prepared (McHugh 1985). The issues are focused on many of the same problems that were germane a decade ago and include the following: 1) an expanded, nondiscriminate, commercial longline fishery, which has the potential to become a huge commercial fishery driven by marketing that portrays "sharks" as a vastly "underutilized" group of species and which includes a longline fishery for other species with an extensive shark bycatch that is considered unimportant by the fishermen, 2) an existing and rapidly expanding recreational fishery, 3) concern for the extensive waste which occurs from both the recreational and commercial activities (especially the rapidly increasing situation of harvesting sharks only for their fins), 4) the reproductive strategy (few offspring, late maturation, and slow growth rates) of many shark species, and 5) realization that increased fishing pressure on specific shark species generally results in overfishing. Overfishing of the recruiting stock (where adults are removed faster than juveniles can replace them) is the result. It occurs because of the life-history strategy of these apex predators. Once a shark species is demonstrated to have been overfished, it is usually too late for management intervention. Recovery may take 25 to 50 years.

Commercial Fishery

The single greatest worldwide use of sharks had been for their meat. World elasmobranch landings are now approaching 600,000 t annually (Compagno 1990). In the United States the public has generally been reluctant to accept shark meat as food, although it is beginning to be found more frequently on restaurant menus and in fish markets. Commercial landings in the United States to date have been small (approximately 3500 t annually) but could be extensively expanded with improved quality in product handling. Currently, the markets are mainly for fresh meat, but urea and TMAO (compounds present in shark blood) cause shark flesh to deteriorate rapidly. Red Lobster Inns of America are extensively using shark as the "fish of the day" while many marketing people are pursuing the school and institutional markets (Cook 1987). Numerous new products like surimi, fish sticks, and shark substitutes for hamburger meat are being continuously proposed. Shark fin soup is one of the most expensive food items in the world—a bowl in the Orient, at times, sells for $20.00.

Commercial landings of "sharks" (all species other than dogfish) in the Atlantic and Gulf regions have been growing steadily during the past decade (Table 1) from around 250 t annually to over 2,000 t with a current associated value of over two and a half million dollars. The reported catch has nearly tripled in the past five years. During the past decade, nearly 90% of the reported commercial landings of unclassified sharks have come from the EEZ. The price per pound of sharks landed in the EEZ is also higher than the price per pound of sharks landed from State controlled waters. The Gulf and South Atlantic regions have shown the most rapid increase and currently have reported landings of around one thousand t each, whereas landings for the Mid-Atlantic region have been rather constant at around 100 t. Although a region's landings may appear constant (e.g., Mid-Atlantic), the individual State's landings within a region may change significantly over time (Table 2). Knowledge and analysis of these fishery shifts may be critical in stock assessments and are critical in management proposals.

The reported commercial landings of sharks, however, exhibit severe limitations in their usefulness for assessment and management analyses relative to many other species. Christensen (Northeast Fisheries Center, Woods Hole, Massachusetts, February 1986) stated that the "commercial

Table 1.
Reported commercial landings (in metric tons) and ex-vessel value (in thousands of dollars) of "unclassified"[a] sharks by region and by distance (in nautical miles) from shore during 1978–1987.[b]

	New England		Mid-Atlantic		South Atlantic		Gulf		Total	
	t	$	t	$	t	$	t	$	t	$
1978										
0–3	8	3	5	4	16	8	10	2	39	17
3–200	18	8	61	9	39	17	87	19	205	53
Total	26	11	66	13	55	25	97	21	245	70
1979										
0–3	3	*[c]	5	3	7	4	5	1	22	8
3–200	22	14	35	15	21	10	35	12	113	51
Total	25	14	40	18	28	14	40	13	135	59
1980										
0–3	25	5	2	2	11	6	8	7	46	20
3–200	155	35	70	20	27	12	160	141	412	208
Total	180	40	72	22	38	18	168	148	458	228
1981										
0–3	10	3	6	3	22	14	37	32	74	52
3–200	173	40	62	14	131	132	225	188	591	374
Total	183	43	68	17	153	146	262	220	666	426
1982										
0–3	1	1	10	5	37	17	30	22	78	45
3–200	97	52	24	34	125	98	267	243	512	427
Total	98	53	34	39	162	115	297	265	590	472
1983										
0–3	4	7	4	2	55	32	72	71	135	112
3–200	52	69	46	63	206	187	286	287	597	606
Total	56	76	50	65	261	219	358	358	724	718
1984										
0–3	2	2	4	4	89	57	23	20	118	83
3–200	47	60	50	87	386	347	245	217	728	711
Total	49	62	54	91	475	404	268	237	846	794
1985										
0–3	2	1	9	4	94	78	21	19	127	102
3–200	33	57	74	143	422	482	314	281	842	963
Total	35	58	83	147	516	560	335	300	969	1065
1986										
0–3	3	3	13	12	73	64	71	44	160	123
3–200	35	75	83	222	552	580	380	385	1050	1262
Total	38	78	96	234	625	644	451	429	1210	1385
1987										
0–3	4	3	13	8	97	64	192	163	305	238
3–200	84	188	102	289	665	757	997	1056	1847	2290
Total	88	191	115	297	762	821	1189	1219	2152	2528

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[a] "Unclassified" sharks does not include dogfish.
[b] Source: Unpubl. prelim. NMFS data.
[c] * = less than $500.

data are poor" and that the "unofficial commercial landings are probably an order of magnitude higher" than those reported in Fishery Statistics of the United States. Christensen's statement represents his personal opinion and is based on the fact that many "sportsmen" sell directly to retail outlets and restaurants, which are outside the normal commercial channels monitored by NMFS or state port agents. The perceived low reporting rate is one of two major problems associated with the commercial records, which are generally the basis for FMP development. The second major problem associated with "sharks" in the U.S. commercial data is the nondifferentiation of species.

Table 2.
Reported commercial landings (in metric tons) and ex-vessel value (in thousands of dollars) of "unclassified"[a] sharks by state and by distance (in nautical miles) from shore during 1978–1987.[b]

	New York		New Jersey		Delaware		Maryland		Virginia	
	t	$	t	$	t	$	t	$	t	$
1978										
0–3	3	4	—[c]	—	—	—	—	—	3	1
3–200	—	—	2	1	—	—	57	8	6	2
Total	3	4	2	1	—	—	57	8	9	3
1979										
0–3	2	2	2	1	—	—	—	—	1	*[d]
3–200	—	—	6	3	—	—	22	3	7	9
Total	2	2	8	4	—	—	22	3	8	9
1980										
0–3	1	2	—	—	—	—	*	*	—	—
3–200	1	1	11	5	—	—	47	7	11	7
Total	2	3	11	5	—	—	47	7	11	7
1981										
0–3	*	*	1	1	4	2	—	—	1	*
3–200	2	2	5	4	—	—	53	7	2	1
Total	2	2	6	5	4	2	53	7	3	1
1982										
0–3	*	1	1	*	1	1	3	1	4	2
3–200	3	7	17	24	—	—	3	2	1	1
Total	3	8	18	24	1	1	6	3	5	3
1983										
0–3	—	—	*	*	—	—	2	1	1	1
3–200	4	9	19	32	—	—	15	18	8	4
Total	4	9	20	32	—	—	17	20	9	5
1984										
0–3	1	1	*	1	—	—	3	2	*	1
3–200	8	26	26	41	—	—	14	18	2	2
Total	9	27	27	41	—	—	17	20	2	3
1985										
0–3	*	1	3	1	4	1	—	—	2	2
3–200	23	67	33	54	—	—	14	17	5	5
Total	23	68	36	55	4	1	14	17	7	7
1986										
0–3	2	6	2	1	3	1	2	2	4	2
3–200	31	92	44	113	—	—	7	15	1	2
Total	33	98	46	114	3	1	9	17	5	4
1987										
0–3	3	3	*	1	—	—	—	—	9	5
3–200	38	94	50	159	—	—	9	24	4	12
Total	41	97	50	159	—	—	9	24	14	17

[a] "Unclassified" sharks does not include dogfish.
[b] Source: Unpubl. prelim. NMFS data.
[c] — = zero.
[d] * = less than $500.

(Beginning in 1987, approximately a dozen of the more common species of sharks were identified as species in the coastal States between Maine and Virginia.)

Although sharks are often lumped together because of difficulties in data collection, often separate fisheries can be differentiated. An initial separation can generally be made between two species assemblages—an inshore shallow water group and an offshore pelagic group. Generally, past directed commercial fisheries have targeted inshore species and have employed bottom longlines or large mesh

Table 3.

Number of sharks taken as bycatch in the Japanese longline fishery in the Northwest Atlantic EEZ, 1982 and 1987.[a]

	January	July	August	September	October	November	December	Total
1982								
Vessels/mongh	—[b]	9	13	11	6	2	6	
Days fished	—	204	301	286	66	31	169	1,057
Species								
Blue shark	—	1,144	1,410	1,550	370	345	1,369	6,188
Hammerhead shark	—	69	25	28	—	—	196	318
Longfin mako	—	—	7	8	—	—	1	16
Shortfin mako	—	38	73	27	19	1	37	195
Unidentified mako	—	63	34	31	5	1	10	144
Bigeye thresher	—	—	1	5	4	2	3	15
Unidentified thresher	—	4	5	10	2	1	1	23
Other sharks	—	13	58	125	10	2	10	218
Total	—	1,331	1,613	1,784	410	352	1,627	7,117
1987								
Vessels/month	7	—	2	2	5	5	7	
Days fished	75	—	51	49	35	142	185	537
Species								
Blue shark	851	—	189	494	936	3,979	827	7,276
Hammerhead shark	0	—	1	3	—	—	15	19
Porbeagle shark	9	—	0	0	2	5	283	299
Great white shark	0	—	0	1	0	0	1	2
Shortfin mako	22	—	64	31	10	105	42	274
Longfin mako	5	—	2	0	0	5	7	19
Unidentified mako	0	—	1	0	3	17	6	27
Bigeye thresher	0	—	20	14	27	53	23	137
Unidentified thresher	0	—	1	23	5	8	7	44
Unidentified shark	55	—	6	1	25	111	35	233
Total	942	—	284	567	1,008	4,283	1,246	8,330

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[a] Source: Observer data summaries from Japanese longline fishery.

[b] — = zero.

gill nets. The pelagic species that have been traditionally landed, are almost exclusively taken as an incidental catch of the longline fishery, although any commercial fishing gear is capable of an incidental catch of sharks. In past years, most of the shark catch was discarded for lack of a market or because of limited fish-hold space, which was generally reserved for more valuable catches. As the market for both shark and other longline species fluctuates, so do the landings for sharks, and since the directed longline fisheries are declining, it is probable that more effort will focus on sharks.

The international commercial catch both inside and outside the U.S. EEZ must be addressed. The recently developing shark fishery of the Yucatan (R. Bonfil, 1987, The shark fishery of Yucatan, Mexico: an introduction and preliminary results. Presentation at 67th annual meeting of American Society of Ichthyologists and Herpetologists, Albany, NY. Author's address: I.N.P. Centro Regional de Investigacion Pesquera de Yucalpeten, A.P. #73, Progreso, Yucatan 67320; and Bonfil et al. 1990), where 2500 t of sharks are harvested annually (some being fished as juveniles), needs to be carefully examined since the same stocks that are being exploited there are probably taken in U.S. fisheries. Foreign longlining inside the EEZ has decreased significantly this decade and the shark catch can be examined through observer reports. Japanese longline fishing activity in the U.S. Atlantic EEZ has decreased from over 1000 days fished in 1982 to only 537 days fished in 1987 (Table 3). However, the U.S. EEZ effort is only about 10 percent of the total Japanese longline fishing effort in the Western North Atlantic. Blue sharks comprise over 80% of the bycatch in the Japanese longline fishery. Mako, hammerhead, and porbeagle sharks also are caught in significant quantities. Species composition from observer reports is important because of the differential associated with mortality of discarded fish. According to Casey (NOAA, Narragansett RI 02882, February 1986) all discarded porbeagle are dead, while nearly 100% of discarded blue sharks are alive when released. Although the foreign longline fishery is decreasing in the U.S. EEZ, the domestic fleet is expanding rapidly. Commercial longlining for tuna, swordfish, and tilefish has grown to the point (250 longline vessels in the Gulf of Mexico alone) where it is probable that the shark bycatch in these fisheries is more extensive than any directed fishery for them.

Recreational Fishery

Recreational fishing for sharks is growing rapidly and has significant economic implications. This growth is best documented in the expanding number of shark tournaments in the Northeast which has grown from 10 in 1980 to 45 in 1985. Recreational tournaments often take 10 to 15 t of sharks (one tournament in Bayshore, NY, killed nearly 1000 blue sharks). However, distributional differences, generally due to the different species preferences in temperature, salinity, and clarity, etc., cause great economic concern among tournament operators, and both commercial and recreational fishermen. The lack of blue sharks in 1984 along the entire New York Bight inshore area may have been caused by very heavy spring rains which may have driven the general inshore populations of blue sharks up to 100 miles offshore. The extensive wide-ranging and highly migratory nature of many shark species must always be remembered in relation to many perceived local population problems.

The recreational fishery is extremely variable geographically. North of Cape Cod, there may be only 50 fishermen that recreationally fish for sharks; whereas between Cape Cod and New York there may be as many as 10,000 fishermen. New Jersey alone may have 10,000 fishermen that target sharks sometime during the year, because sharks are often the only large pelagic species available during June and July. In Florida, sharks are often the focus of a major charter boat fishery, and in South Carolina, there are several tournaments and a significant directed shark fishery. Available much closer to shore (the majority of fishing occurs between 15 and 30 miles offshore), sharks are plentiful to a far greater number of anglers than are billfish and tuna.

Data available from the annual Marine Recreational Fishery Statistics Survey (MRFSS) are extremely variable (Table 4) among years, which is not surprising considering sharks are viewed as a "rare event" in the survey (M. Holliday, NMFS, Silver Spring MD, 20910, pers. commun., February, 1986). Standard error estimates for the total number of sharks caught in the entire Atlantic range from about 10% to nearly as much as 50% of the number estimate. Standard error estimates at times exceed the number estimate on a regional basis. Despite the imprecision of the estimates, several very interesting trends appear. First, about 2.5 million sharks (excluding dogfish) are caught annually by marine anglers. Second, the associated weight of the catch is around 35,000 t annually. Third, there is much less variability around the catch that has been killed than around the total catch. There are around three-quarters of a million fish killed annually. Fourth, the estimated number of sharks killed annually (Type A and B1; where A is catch available for identification to an interviewer and B1 is catch identified by a fisherman as filleted, discarded dead, or used as bait, as opposed to Type B2, where the catch is classified as being released alive) varies from 20% to about 45% but is always less than half the total estimated catch (Table 4).

Recent changes in MRFSS's distribution of interviews has resulted in increased coverage of interviews with boat fishermen (M. Holliday, NOAA, Silver Spring MD 20910, pers. commun., February 1986). This increased frequency of sampling should provide considerably better shark data and may provide much more accurate estimates of the catch, especially for the more common species. More than two thirds of the annual recreational catch has always been made from boats (Table 5). More than half the recreational catch is taken from private or rental boats rather than from party or charter vessels.

Shortfin mako was the dominant (by weight) species of shark (excluding dogfish) caught by recreational fishermen during the first six years of the MRFSS (Table 6). Sandbar, blue, and dusky sharks also appeared to be caught in large quantities. The best feature of the MRFSS is that individual species of sharks are identified, compared to the commercial data, where "sharks" encompass all species except dogfish. The difficulty is in extrapolating from the actual number of sharks in each category caught (Table 7) to the total numbers of fish. While the MRFSS is valuable in permitting actual identification to species and in providing some data on the length and weight by species, it is obvious that some form of expanded survey is necessary to describe such "rare event" species as sharks.

Waste

Although the importance of immediate quality care is recognized as needed in handling sharks and the general perception of sharks as underutilized is accepted, many of the sharks caught are actually wasted. Many species (e.g., hammerheads) are killed simply for their fins and the remainder of the carcass is discarded. In the South Atlantic area, for example, the largest source of fishing mortality among the offshore shark species is from the swordfish longline fishery, and only a very small percentage of the sharks caught as a bycatch are ever landed. Much of the recreational kill is made simply for photographing, the result being that the fish are deposited in landfills. The release of live sharks not intended for consumption or science should be encouraged.

Reproductive Strategy

The biological adaptation of elasmobranchs to their ecological niche has created the greatest concern relative to

Table 4.
Summary of estimated catches of sharks (excluding dogfish) taken by marine recreational fishermen, by region, 1979–87. Number caught is × 1000; mean wt. is in kg; total wt. in t. Standard errors in parentheses.[a]

	North Atlantic		Mid-Atlantic		South Atlantic		Gulf		Atlantic totals	
1979										
# caught	—[b]	—	889	(134)	448	(113)	779	(104)	2,119	(204)
# killed	—	—	388	(73)	191	(48)	268	(52)	847	(102)
Mean wt.	—		76.4		2.7		4.4		37.5	
Total wt.	—		67,920		1,210		3,428		79,463	
1980										
# caught	82	(29)	1,712	(213)	517	(81)	764	(169)	3,075	(285)
# killed	56	(28)	203	(43)	268	(53)	235	(48)	761	(88)
Mean wt.	—		2.4		10.6		8.4		7.9	
Total wt.	—		4,109		5,480		6,418		24,293	
1981										
# caught	—	—	315	(65)	691	(822)	892	(342)	1,906	(893)
# killed	—	—	63	(24)	121	(56)	519	(327)	707	(332)
Mean wt.	—		9.3		22.2		18.1		18.2	
Total wt.	—		2,930		15,340		16,145		34,689	
1982										
# caught	48	(18)	550	(265)	419	(46)	452	(72)	1,469	(279)
# killed	—	—	183	(87)	248	(34)	197	(29)	632	(98)
Mean wt.	—		11.5		6.3		5.2		7.5	
Total wt.	—		6,325		2,640		2,350		11,018	
1983										
# caught	47	(25)	4,504	(1341)	783	(161)	308	(55)	5,641	(1352)
# killed	—	—	515	(87)	386	(141)	188	(46)	1,106	(172)
Mean wt.	—		9.4		7.7		1.8		9.0	
Total wt.	—		42,388		6,029		554		50,769	
1984										
# caught	285	(59)	1,350	(222)	728	(113)	423	(73)	2,786	(267)
# killed	52	(17)	326	(80)	232	(47)	220	(55)	830	(109)
Mean wt.	—		9.4		2.9		1.4		5.2	
Total wt.	—		12,690		2,111		592		14,487	
1985										
# caught	—	—	437	(87)	548	(67)	772	(142)	1,774	(180)
# killed	—	—	97	(23)	264	(42)	446	(126)	809	(135)
Mean wt.	—		37.3		10.4		6.6		11.8	
Total wt.	—		16,300		5,699		5,095		20,933	
1986										
# caught	33	(12)	1,141	(371)	452	(72)	695	(71)	2,322	(385)
# killed	—	—	160	(56)	100	(18)	322	(47)	588	(76)
Mean wt.	—		31.3		12.1		12.9		21.4	
Total wt.	—		35,713		5,469		8,966		49,691	
1987										
# caught	33		59		767		631		2,026	
Mean wt.	—		36.9		6.6		5.1		10.3	
Total wt.	—		22,029		5,062		3,218		20,868	

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[a] Source: USDC, 1988.
[b] — = zero.

fishing, because the life history strategy of these species does not lend itself to high exploitation (Anderson 1990; Branstetter 1990; Cailliet et al. 1990; Compagno 1990; Hoenig and Gruber 1990; Ishihara 1990; Pratt and Casey 1990; and Otake 1990). One of the most significant factors in the reproductive success of many sharks is their ability to give birth to live young. However, the evolutionary trade-off of giving birth to well developed young is that very few progeny can be born (Pratt and Casey 1990). The low reproductive potential is also associated with long gestation periods (up to two years), pupping in alternate years, late maturity, and slow growth rate. Sharks lack bony parts and often exhibit tremendous growth variability in their cartilaginous structure, thus making ageing extremely

Table 5.
Estimated total number (× 1000) of sharks (exclusing dogfish) caught by marine recreational fishermen, by mode of fishing, by region, 1979–1986.[a]

	North Atlantic	Mid-Atlantic	South Atlantic	Gulf	Atlantic totals
1979					
Shore	—[b]	—	—	251	250
Party/charter	*[c]	132	—	112	255
Private rental	*	723	386	416	1,524
Total	—	889	448	779	2,119
1980					
Shore	—	185	187	90	575
Party/charter	—	88	—	37	170
Private rental	51	1,339	303	637	2,331
Total	82	1,712	517	764	3,075
1981					
Shore	—	—	374	238	614
Party/charter	—	119	—	298	418
Private rental	—	195	316	356	874
Total	—	315	691	892	1,906
1982					
Shore	—	—	95	100	242
Party/charter	—	358	—	98	485
Private rental	32	163	294	254	742
Total	48	550	419	452	1,469
1983					
Shire	—	1,509	212	58	1,801
Party/charter	—	144	41	63	248
Private rental	44	2,851	529	167	3,592
Total	47	4,504	783	308	5,641
1984					
Shire	—	104	243	73	464
Party/charter	55	248	—	39	367
Private rental	225	976	459	296	1,956
Total	285	1,350	728	423	2,786
1985					
Shore	—	—	108	61	201
Party/charter	—	44	111	37	193
Private rental	—	376	328	662	1,380
Total	—	437	548	772	1,774
1986					
Shore	—	49	106	—	168
Party/charter	—	61	—	—	111
Private rental	—	1,031	319	665	2,043
Total	33	1,141	452	695	2,322

[a] Source: USDC, 1988.
[b] — = less than 30,000 kg reported.
[c] * = zero.

difficult. The difficulty of making accurate age estimates coupled with the lack of fishery data (since few directed shark fisheries exist) have inhibited comprehensive biological understanding. Since so little has been known of many stocks (their population dynamics and even life history characteristics), management for the rational exploitation of elasmobranchs has been extremely difficult.

Fishing Pressure

It cannot be over emphasized that sharks are in a precarious position and cannot be treated the same as teleost stocks. Commercial exploitation directed at single elasmobranch species inevitably leads to rapid decline of those stocks and sooner or later to a dramatic collapse of the fishery (Ripley 1949; Olsen 1959; Holden 1968; Casey et al. 1978; Anderson 1990; Taniuchi 1990; and Pratt and Casey 1990).

Table 6.

Species weight (× 1000 kg) and percentage of Mid-Atlantic shark catch in the recreational fishery, 1979–1984.[a]

	1979		1980		1981		1982		1983		1984	
	Wt.	%	Wt.	%	Wt.	%	Wt.	%	Wt.	%	Wt.	%
Requiem sharks	508	2	4	1	3	*[b]	—[c]	—	—	—	—	—
Blue shark	6,168	26	—	—	389	42	—	—	—	—	68	2
Shortfin mako	10,785	45	186	53	74	8	1,475	53	1,480	55	2,593	91
Tiger	3,073	13	—	—	—	—	—	—	—	—	—	—
Dusky	1,854	8	16	5	69	7	—	—	353	13	25	1
Sandbar	687	3	81	23	66	7	38	1	472	18	58	2
Mackerel sharks	618	3	—	—	—	—	—	—	—	—	—	—
Scalloped hammerhead	210	1	—	—	—	—	—	—	—	—	—	—
Bonnethead	165	1	—	—	—	—	—	—	—	—	—	—
Sand tiger	9	*	31	9	22	2	1,157	42	343	13	—	—
Bull	8	*	—	—	—	—	89	3	—	—	—	—
Sharpnose	—	—	1	*	—	—	—	—	—	—	—	—
Blacktip	—	—	42	12	—	—	—	—	—	—	—	—
Lemon	—	—	—	—	304	33	—	—	—	—	—	—
Smooth hammerhead	—	—	—	—	—	—	—	—	31	1	—	—
White	—	—	—	—	—	—	—	—	—	—	108	4
Total	24,085	100	351	100	927	100	2,759	100	2,679	100	2,852	100

[a] Source: Unpubl. prelim. NMFS data.

[b] * = less than 0.5%.

[c] — = zero.

Documented collapses in the shark population and the shark fishery include the California soupfin and thresher shark fisheries, the basking shark off Scotland, the Norwegian and Faroese porbeagle fisheries in the Western North Atlantic, the Australian school shark fishery, the Scottish-Norwegian spiny dogfish fishery, the Japanese spiny dogfish fishery, and most recently the blue shark off Catalina Island in California.

National Standards

All FMP's prepared under the MFCMA must be consistent with seven national standards (section 301) for fishery conservation and management (Table 8). Of the seven standards, the first three (overfishing and optimum yield, best scientific information, and management as a unit) are most germane to the shark FMP issues.

Overfishing and Optimum Yield (OY)

An FMP must contain an OY estimate, which in general must be based on an estimate of maximum sustainable yield (MSY). The determination of OY is a decisional mechanism for resolving the MFCMA's multiple purposes and policies for implementing an FMP's objectives, and for balancing the various interests that comprise the national welfare. The most important limitation on the specification of an OY is that it and the conservation and management measures proposed to achieve it must prevent overfishing. Overfishing is defined as a state in which fishing mortality has reduced a stock to such a size that it can not produce maximum biological yield or economic value on a long-term basis under prevailing biological and environmental conditions.

The MSY (Otto et al. 1977) for pelagic sharks in the Atlantic, north of the equator and west of 40 degrees, was determined to be 41,000 t in the original PMP, based on a Schaefer yield curve which reflected historical catch/effort information from recreational and commercial fishing in the North Atlantic. The PMP Amendment committee drafters (U.S. Dep. Commer. 1982) reviewed more recent information on shark fishing in the Western North Atlantic and concluded that there was no basis to revise the MSY despite the obvious limitations. Determination of the MSY for pelagic sharks in the U.S. Atlantic EEZ is confounded by a variety of factors. Many species of sharks are included in the overall harvest; thus statistics for individual species of sharks are not available. There are about 350 species of sharks worldwide (Compagno 1984) and at least 100 species that occur in the Atlantic EEZ. Sharks are generally wide- ranging in distribution, discrete stocks are not confined to waters of the EEZ, and information is lacking on which to base any delimitation of individual stocks. Reported catches of pelagic sharks represent, at best, only a limited portion of the total mortality. Reliable fishing

Table 7.

Number of intercepts with sharks and actual number of sharks caught from the MRFSS, by species, 1979–84.[a]

Species/family	# Intercepts with sharks A[b]	B1	B2	# Caught A	B1	B2
Cowsharks	—	—	1	—	—	1
Whale sharks	—	—	1	—	—	1
Carpet sharks	—	—	3	—	—	6
Nurse shark	9	4	24	10	7	31
Sand tiger sharks	1	3	3	1	13	3
Sand tiger shark	29	37	124	40	73	378
Mackerel sharks	3	1	2	8	5	3
White shark	1	1	2	1	1	2
Basking shark	—	—	1	—	—	1
Porbeagle	—	—	1	—	—	1
Thresher shark	1	3	3	1	4	3
Shortfin mako shark	37	6	9	39	8	9
Cat/requiem/hammerhead sharks	2	16	37	2	27	58
Catsharks	—	2	17	—	9	47
Requiem sharks	27	54	224	69	194	629
Tiger shark	16	4	7	16	5	10
Atlantic sharpnose shark	34	20	54	93	81	227
Mustelus spp.	—	—	6	—	—	8
Smooth dogfish	134	105	595	268	275	1,823
Florida smoothound	3	1	5	4	3	10
Brown smoothhound	—	5	5	—	9	11
Carcharhinus spp.	4	5	31	4	9	100
Dusky shark	53	13	38	78	27	101
Bull shark	23	11	20	36	49	36
Sandbar shark	126	95	416	245	282	1,129
Blacknose shark	6	—	1	10	—	4
Bignose shark	—	—	1	—	—	1
Silky shark	12	2	1	19	6	1
Blacktip shark	75	49	117	156	95	366
Ocean whitetip shark	—	—	1	—	—	1
Spinner shark	6	3	5	9	6	9
Reef shark	—	—	3	—	—	6
Blue shark	22	6	53	23	33	106
Night shark	1	—	—	1	—	—
Lemon shark	21	3	21	25	5	45
Finetooth shark	1	—	—	1	—	—
Hammerhead shark	13	10	38	130	19	68
Sphyrna spp.	10	7	34	15	12	56
Bonnethead shark	49	18	60	70	34	105
Smooth hammerhead	5	—	4	8	—	8
Scalloped hammerhead	33	4	20	54	5	58
Great hammerhead	14	20	43	16	22	79
Smalleye hammerhead	—	1	—	—	1	—
Total	761			1,180		

[a] Source: Unpubl. prelim. NMFS data.
[b] A = Catch available for identification.
B1 = Used for bait, filleted, discarded dead, etc.
B2 = Released alive.
[c] — = zero.

effort or catch per effort data for sharks is lacking. A suitable data base and appropriate model are lacking to determine properly the MSY for sharks in the western North Atlantic and more particularly in the U.S. EEZ within this overall region (Anderson 1980). Anderson (1980) estimates that sharks in the Atlantic may well be excessively exploited. However, since catch rates for individual species are lacking, this probability cannot be

Table 8.
National Standards for Fishery Conservation and Management.

IN GENERAL. Any fishery management plan prepared, and any regulation promulgated to implement any such plan, pursuant to this title shall be consistent with the following national standards for fishery conservation and management:

(1) Conservation and management measures shall prevent overfishing while achieving, on a continuing basis, the optimum yield from each fishery for the United States fishing industry.

(2) Conservation and management measures shall be based upon the best scientific information available.

(3) To the extent practicable, an individual stock of fish shall be managed as a unit throughout its range, and interrelated stocks of fish shall be managed as a unit or in close coordination.

(4) Conservation and management measures shall not discriminate between residents of different States. If it becomes necessary to allocate or assign fishing privileges among various United States fishermen, such allocation shall be (A) fair and equitable to all such fishermen; (B) reasonably calculated to promote conservation; and (C) carried out in such manner that no particular individual, corporation, or other entity acquires an excessive share of such privileges.

(5) Conservation and management measures shall, where practicable, promote efficiency in the utilization of fishery resources; except that no such measure shall have economic allocation as its sole purpose.

(6) Conservation and management measures shall take into accout and allow for variations among, and contingencies in, fisheries, fishery resources, and catches.

(7) Conservation and management measures shall, where practicable, minimize costs and avoid unnecessary duplication.

confirmed. Anderson (1980) concluded: "It may be advisable to limit further increases in catch, and possibly initiate measures to reduce bycatch, particularly in the several domestic and foreign longline fisheries."

Best Available Data

The fact that scientific information concerning a fishery is incomplete does not prevent the preparation and implementation of an FMP. An FMP must specify the information fishermen and processors will be required or requested to submit. An FMP should identify scientific information needed from other sources to improve understanding and management of the resource and the fishery.

Management Units

An individual stock of fish shall be managed as a unit throughout its range, and interrelated stocks of fish shall be managed as a unit or in close coordination. The purpose of this standard is to induce a comprehensive approach to fishery management. Cooperation and understanding among entities concerned with the fishery (e.g., Councils, States, Federal Government, international commissions, and foreign nations) are vital to effective management. FMPs should include conservation and management measures for that part of the management unit within U.S. waters. A management unit may contain, in addition to regulated species, stocks of fish for which there is not enough information available to specify MSY and OY or to establish management measures, so that data on these species may be collected under the FMP. Guidelines for this national standard allow for the estimation of MSY for the entire stock and base the determination of OY for the U.S. fishery on the portion of the stock within U.S. waters as was done by Anderson (1980, e.g., 15% of total MSY or 6,150 t).

Panel of Shark Experts

A panel consisting of individuals from academia, NMFS, and the Councils was convened in 1986 in response to the needs of the Inter-Council Shark Committee. Participants included J. Musick, S. Gruber, J. Castro, E. Houde, F. Schwartz, and S. Branstetter from academia; J. Casey, M. Holliday, R. Stone, and M. Parrack from NMFS; and B. Freeman, S. Berkeley, P. Hooker, and T. Hoff from the Councils. The principal charge to the Panel was to assemble and review existing information on sharks in the Western North Atlantic. The Shark Committee was to use the information collected to determine whether an FMP should be undertaken or if not, what action should occur.

The Panel addressed the existing state of knowledge through completion of an information matrix covering the commonly occurring species in the five geographical regions (Tables 9–13). Definition of the commonly occurring species was reached by consensus and the degree of knowledge about them was ranked 0, 1, or 2, depending upon whether there was no knowledge, some knowledge, or considerable knowledge (not necessarily sufficient for stock assessment).

Considerable information exists about much of the general biology for many of the commonly occurring

Table 9.
The general state of knowledge for the abundant species of sharks in the western North Atlantic, for the New England area—Cape Cod and North. The listings are general categories of information where each category of information for each species listed is ranked as follows: (0) no information known, no data available; (1) some information known, data available in either published or unpublished form; and (2) considerable information known, data available either published or unpublished form.

	Blue	Porbeagle	Shortfin mako	Basking
Food habits	2	2	2	2
Distribution	2	2	2	2
Migratory route	2	1	1	2
Nursery areas	1	0	0(?)	1
Growth	2	2	2	2
Age at size	2	2	2	2
Size frequency	2	2	2	2
Reproductive rate	2	1	1	0
Commercial landings	0(a)	1	1	0(a)
Recreational landings	2	0(c)	2	0(c)
Catch effort	1	1	1	0(a)
Discard rate	1(b)	0	2	NA
Age frequency	2	1	1	2
Stock structure	2	0	0	1
Mortality	1	0	0	1
Recruitment	0	0	0	0
Yield/recruit	0	0	0	0
Virtual population analysis	0	0	0	0
Predictive models	0	0	0	0

(a) No directed commercial fishery in western North Atlantic.
(b) A lack of information exists in the catch of the domestic fishery but the nondirected catch believed to be significant.
(c) No directed recreational fishery in the western North Atlantic.
NA Not applicable.
(?) Not sure.

species, e.g., food habits, size frequency, growth, age at size, and distribution (Tables 9–13). Certainly much less information is known about fishery operations (commercial and recreational landings, catch/effort, discard and mortality rates). There is inadequate management information available (stock structure, stock-recruitment relationship, yield per recruit, output from predictive models or virtual population analysis) for nearly all species.

It was agreed by the Panel that it would be very difficult, based upon the present state of knowledge, to write an FMP to regulate a single shark species, or even a species group (Freeman 1986). It was judged that the existing management information was not adequate to realistically write such a plan. A lot of information and data on the biology of sharks have been collected by several individuals and institutions but are scattered up and down the coast. This type of information will need to be assembled, collated, and analyzed in order to be useful to management. A single "pelagic" management plan which included billfish and perhaps tuna would not reasonably lend itself to include all the common shark species. Many species do not lend themselves to a "pelagic" plan because they are rarely caught in the offshore longline fishery (e.g., sandbar, sharpnose, and lemon). It was recommended that three shark species be chosen and closely monitored in order to develop models for plan preparation. These species should be representative of the shark species occurring off the Atlantic and should be species for which considerable knowledge presently exists on their life history. Sandbar (inshore and midshelf), blue (wide-ranging, oceanic), and either the silky or blacktip (common in southern waters) were the species suggested. Mako was considered since public concern for this species is providing the impetus for management attempts. However, very little information is known about mako sharks (Freeman 1986).

The Panel determined that sharks comprise a large, widely diverse group of fishes. Some species conveniently fall into a pelagic grouping: blue, mako, silky, night, oceanic whitetip, bigeye thresher, porbeagle, and longfin and shortfin mako. An inshore group would include sandbar, smooth dogfish, sand tiger, blacktip, blacknose, sharpnose and bull sharks. The third group falls between oceanic

Table 10.

The general state of knowledge for the abundant species of sharks in the western North Atlantic, for the Middle Atlantic area—Cape Cod to Cape Hatteras. The listings are general categories of information where each category of information for each species listed is ranked as follows: (0) no information known, no data available; (1) some information known, data available in either published or unpublished form; and (2) considerable information known, data available either published or unpublished form.

	Inshore 0–40 fathoms									
	Sandbar	Dusky	Atlantic sharpnose	Sand tiger	Smooth dogfish	Scalloped hammerhead	Tiger	Blacktip	Shortfin mako	Bull
Food habits	2	2	2	2	2	1	2	2	2	2
Distribution	2	1	2	1	2	1	2	2	2	2
Migratory route	2	1	0	1	1	1	1	1	1	2
Nursery areas	2	2	2	1	1	1	1	2	0(?)	2
Growth	2	2	2	1	1	2	2	2	2	2
Age at size	2	2	2	1	1	2	2	2	2	2
Size frequency	2	1	2	1	1	1	1	2	2	2
Reproductive rate	1	1	2	2	1	1	2	2	1	2
Commercial landings	0	0	0	0(b)	0(b)	0	0(b)	0(b)	1	1
Recreational landings	1	1	0(b)	1	2	2	1	1	2	1
Catch effort	1	1	2	0	0	1	1	1	1	1
Discard rate	NA	0	0(b)	NA	0(b)	1	2	1	2	1
Age frequency	2	2	2	1	1	2	2	2	1	2
Stock structure	1	0	0	0	0	0	0	0	0	0
Mortality	0	0	0	0	0	0	0	0	0	0
Recruitment	0	0	0	0	0	0	0	0	0	0
Yield/recruit	0	0	0	0	0	0	0	0	0	0
Virtual population analysis	0	0	0	0	0	0	0	0	0	0
Predictive models	0	0	0	0	0	0	0	0	0	0

	Offshore 40–1,000 fathoms					
	Blue	Silky	Scalloped hammerhead	Bignose	Night	Longfin mako
Food habits	– 2	1	1	1	1	1
Distribution	2	1	1	1	1	1
Migratory route	2	1	1	1	1	0(?)
Nursery areas	1	1	1	1	1	0
Growth	2	2	2	1	1	0
Age at size	2	1	2	1	1	0
Size frequency	2	2	1	1	1	0
Reproductive rate	2	1	1	0	1(?)	1
Commercial landings	0(a)	0(a)	0	0	1	0(?)
Recreational landings	2	0	2	0	1	0
Catch effort	1	1	1	0	1	0
Discard rate	1(b)	0(a)	1	0	0	0
Age frequency	2	2	2	1	1	0
Stock structure	2	0	0	0	0	0
Mortality	1	0	0	0	0	0
Recruitment	0	0	0	0	0	0
Yield/recruit	0	0	0	0	0	0
Virtual population analysis	0	0	0	0	0	0
Predictive models	0	0	0	0	0	0

(a) No directed commercial fishery in western North Atlantic.
(b) A lack of information exists in the catch of the domestic fishery but the nondirected catch believed to be significant.
(c) No directed recreational fishery in the western North Atlantic.
NA Not applicable.
(?) Not sure.

Table 11.

The general state of knowledge for the abundant species of sharks in the South Atlantic area—Cape Hatteras to Key West. The listings are general categories of information where each category of information for each species listed is ranked as follows: (0) no information known, no data available; (1) some information known, data available in either published or unpublished form; and (2) considerable information known, data available either published or unpublished form.

Inshore 0–40 fathoms

	Atlantic sharpnose	Black-nose	Sandbar	Scalloped hammerhead	Dusky	Silky	Tiger	Sand tiger	Black-tip	Spinner	Bull	Nurse	Lemon
Food habits	2	1	2	1	2	1	2	2	2	2	2	2	2
Distribution	2	2	2	1	1	1	2	1	2	2	2	2	2
Migratory route	0	1	2	1	1	1	1	1	1	1	2	2	2
Nursery areas	2	2	2	1	2	1	1	1	2	2	2	2	2
Growth	2	2	2	2	2	2	2	1	2	2	2	2	2
Age at size	2	2	2	2	2	1	2	1	2	2	2	2	2
Size frequency	2	2	2	1	1	2	1	1	2	1	2	2	2
Reproductive rate	2	2	1	1	1	1	2	2	2	2	2	2	2
Commercial landings	0	0(b)	0	0	0	0(a)	0(b)	0(b)	0(b)	1	1	0(b)	0
Recreational landings	0(b)	0(b)	1	2	1	0	2	1	1	1	1	1	2(?)
Catch effort	2	1	1	1	1	1	1	0	1	1	1	1	1
Discard rate	0(b)	0(b)	NA	1	0	0(a)	0(b)	NA	1	0(b)	1	0(b)	0
Age frequency	2	2	2	2	2	2	2	1	2	2	2	0(?)	2
Stock structure	0	0	1	0	0	0	0	0	0	0	0	0	0
Mortality	0	0	0	0	0	0	0	0	0	0	0	0	1
Recruitment	0	0	0	0	0	0	0	0	0	0	0	0	1
Yield/recruit	0	0	0	0	0	0	0	0	0	0	0	0	0
Virtual population analysis	0	0	0	0	0	0	0	0	0	0	0	0	0
Predictive models	0	0	0	0	0	0	0	0	0	0	0	0	0

Offshore 40–1,000 fathoms

	Scalloped hammerhead	Dusky	Silky	Night	Bignose	Bigeye thresher	Blue	Tiger	Lemon	Oceanic whitetip
Food habits	1	2	1	1	1	2	2	2	2	1
Distribution	1	1	1	1	1	2	2	2	2	2
Migratory route	1	1	1	1	1	1	2	1	2	0
Nursery areas	1	2	1	1	1	0	1	1	2	0(?)
Growth	2	2	2	1	1	2	2	2	2	0
Age at size	2	2	1	1	1	2	2	2	2	0
Size frequency	1	1	2	1	1	1	2	1	2	0
Reproductive rate	1	1	1	1(?)	0	2	2	2	2	1
Commercial landings	0	0	0(a)	1	0	1	0(a)	0(b)	0	0
Recreational landings	2	1	0	1	0	0	2	2	2(?)	0
Catch effort	1	1	1	1	0	1	1	1	1	0
Discard rate	1	0	0(a)	0	0	0(b)	1(b)	0(b)	0	0(b)
Age frequency	2	2	2	1	1	1(?)	2	2	2	0
Stock structure	0	0	0	0	0	0	2	0	0	0
Mortality	0	0	0	0	0	0	1	0	1	0
Recruitment	0	0	0	0	0	0	0	0	1	0
Yield/recruit	0	0	0	0	0	0	0	0	0	0
Virtual population analysis	0	0	0	0	0	0	0	0	0	0
Predictive models	0	0	0	0	0	0	0	0	0	0

(a) No directed commercial fishery in western North Atlantic.
(b) A lack of information exists in the catch of the domestic fishery but the nondirected catch believed to be significant.
(c) No directed recreational fishery in the western North Atlantic.
NA Not applicable.
(?) Not sure.

Table 12.

The general state of knowledge for the abundant species of sharks in the Gulf of Mexico. The listings are general categories of information where each category of information for each species listed is ranked as follows: (0) no information known, no data available; (1) some information known, data available in either published or unpublished form; and (2) considerable information known, data available either published or unpublished form.

	Inshore 0–40 fathoms				
	Atlantic sharpnose	Blacktip	Bull	Sandbar	Spinner
Food habits	2	2	2	2	2
Distribution	2	2	2	2	2
Migratory route	0	1	2	2	1
Nursery areas	2	2	2	2	2
Growth	2	2	2	2	2
Age at size	2	2	2	2	2
Size frequency	2	2	2	2	1
Reproductive rate	2	2	2	1	2
Commercial landings	0	0(b)	1	0	1
Recreational landings	0(b)	1	1	1	1
Catch effort	2	1	1	1	1
Discard rate	0(b)	1	1	NA	0(b)
Age frequency	2	2	2	2	2
Stock structure	0	0	0	1	0
Mortality	0	0	0	0	0
Recruitment	0	0	0	0	0
Yield/recruit	0	0	0	0	0
Virtual population analysis	0	0	0	0	0
Predictive models	0	0	0	0	0

	Offshore 40–1,000 fathoms						
	Silky	Scalloped hammerhead	Dusky	Tiger	Night	Smooth dogfish	Oceanic whitetip
Food habits	1	1	2	2	1	2	1
Distribution	1	1	1	2	1	2	2
Migratory route	1	1	1	1	1	1	0
Nursery areas	1	1	2	1	1	1	0(?)
Growth	2	2	2	2	1	1	0
Age at size	1	2	2	2	1	1	0
Size frequency	2	1	1	1	1	1	0
Reproductive rate	1	1	1	2	1(?)	1	1
Commercial landings	0(a)	0	0	0(b)	0	0(b)	0
Recreational landings	0	2	1	2	1	2	0
Catch effort	1	1	1	1	1	0	0
Discard rate	0(a)	1	0	0(b)	0	0(b)	0(b)
Age frequency	2	2	2	2	1	1	0
Stock structure	0	0	0	0	0	0	0
Mortality	1	0	0	0	0	0	0
Recruitment	0	0	0	0	0	0	0
Yield/recruit	0	0	0	0	0	0	0
Virtual population analysis	0	0	0	0	0	0	0
Predictive models	0	0	0	0	0	0	0

(a) No directed commercial fishery in western North Atlantic.
(b) A lack of information exists in the catch of the domestic fishery but the nondirected catch believed to be significant.
(c) No directed recreational fishery in the western North Atlantic.
NA Not applicable.
(?) Not sure.

Table 13.

The general state of knowledge for the abundant species of sharks in the Caribbean (shore to 40 fathoms). The listings are general categories of information where each category of information for each species listed is ranked as follows: (0) no information known, no data available; (1) some information known, data available in either published or unpublished form; and (2) considerable information known, data available either published or unpublished form.[a]

								Hammerhead							
	Black-tip	Sand-bar	Reef	Small-tail	Lemon	Nurse	Sharp-nose	Small-eye	Scoop-head	Scalloped	Great	Bonnet-head	Narrowfin smooth-hound	Dusky	Dagger-nose
Food habits	0	0	0	1	2	2	1	1	1	1	1	1	1	1	0
Distribution	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Migratory route	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Nursery areas	0	0	0	1	2	2	1	1	0	1	1	1	0	1	0
Growth	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Age at size	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Size frequency	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Reproductive rate	1	0	1	1	2	0	1	1	1	1	1	1	1	1	0
Commer. landings	1	0	0	1	0	0	1	1	1	1	0	0	0	0	0
Recrea. landings	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Catch effort	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0
Discard rate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age frequency	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Stock structure	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mortality	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Recruitment	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yield/recruit	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Virt. pop. analysis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Predictive models	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[a] Information exists for some of these species (e.g., blacktip, sandbar) in northern latitudes. It is likely that Caribbean sharks belong to different stocks than those found off the East Coast but this needs to be determined. (Source: Castro, personal commun.)

and inshore and would include bignose, scalloped hammerhead, dusky, and tiger (Freeman 1986).

Recommended Data Needs

Significant information required for stock assessment is lacking for sharks and thus management is severely handicapped. Meaningful assessments of shark populations in the western North Atlantic are difficult for a variety of reasons: 1) There has never been a directed fishery for sharks sizeable enough to produce landings (except for possibly porbeagles) that might reflect the potential sustainable yield—most shark catches have been incidental to other fisheries; and 2) many, probably most, of the sharks taken as incidental catches in U.S. fisheries have been discarded. Tag return data indicate that most species undergo extensive migrations. The actual distributions of age and sexes in the population are often difficult to ascertain. In addition, many species have seasonal movements that differ between sexes, and nursery areas may be a thousand miles from adult winter foraging areas (Musick and Colvocoresses 1988).

Current data needs can generally be grouped into the three categories that were used by the Shark Panel to describe the state of shark knowledge: biology, fishery, and assessment/management. In addition, all FMPs need to contain social and economic data to address issues of management impact. It must be emphasized that the data needed in these four categories are not exclusive of each other.

Biological Information

Mapping the inshore pupping and nursery grounds is critical, especially because of the potential for direct stock and recruitment relationships. Valid age and growth information for each species is critical. These data can be obtained from studies of seasonal growth rings on vertebrae or spines, from size frequency, aquarium studies, oxytetracycline marking, or tag and recapture experiments (Cailliet 1990). Age- and sex-related distribution and migrations in time and space need to be better delineated for many species, such as sandbar sharks which have their nursery area in the mid Atlantic but which have large concentrations of males off Mexico (Bonfil et al. 1990). Stock differentiation is necessary to determine if species such as blacktips have different stocks in the Caribbean and the South Atlantic, or others, such as duskies, may have only one population that occurs over the entire western North Atlantic.

Almost any information on natural mortality would prove insightful.

Fisheries Information

A statistically valid sample to describe the catch by species is critical. Managers must know annually how many sharks are killed (landed and discarded) and from what geographical locations. The entire range must be represented, e.g., U.S. EEZ, beyond the EEZ, State waters, Caribbean EEZ, Mexican waters, and South American waters of the Caribbean. The total catch from both commercial and recreational fishermen, as well as fishing effort (catch per unit effort) is mandatory.

Fishery sampling data (length, weight, sex, age, and maturity) will be required for any valid stock assessment. Total mortality, fishing mortality and nearly all information obtained from an assessment are contingent on these data.

Tagging studies within the various fisheries are important (Casey and Taniuchi 1990), and efforts need to be expended on better methods of identification of sharks in the water for all the nontrained scientific personnel that contribute, since misidentification greatly affects the reliability of statistical information. All information from the numerous tagging efforts should be centralized because the data provide needed information on migrations and stock identity. Tagging studies focused on key species may provide fishing mortality rates which can answer questions about how severe the situation is right now.

Assessment/Management Information

Independent fishery indices of shark population abundance through time are critical. Longline survey data from National Marine Fisheries Service, Virginia Institute of Marine Sciences, foreign longline fisheries, etc., need to be analyzed for long-term trends in abundance.

Different population models and assessment approaches are necessary for sharks because their life history strategies differ so drastically from most teleost fishes (Anderson 1990).

Socio-Economic Information

An organized effort is needed to collect social and economic information, both in the recreational and the commercial fisheries. The number of fishermen who fish for sharks, the location, the income spent on shark fishing, and how much of a commercial fisherman's income is derived from fishing for sharks are minimum data necessary for a plan. Documentation of all user groups (recreational, commercial, national, and foreign) is needed.

Summary

There has been a rapid expansion in both the recreational effort directed towards sharks and in the reported commercial landings of sharks. The swordfish and tuna longline fisheries are more extensive and involve more discarded shark waste than any currently directed shark fishery. The low rate of replacement and slow growth rates of many species contribute directly to the problem of increased fishing pressure, rapidly resulting in over-exploitation. Fisheries data are becoming better, but a documentation of the catch is probably the most important element needed. Access to the foreign swordfish and tuna longline data both inside the EEZ and beyond 200 miles is necessary for any valid analysis of the stocks. Cooperation among all countries fishing in the Gulf of Mexico is also required. Inter-jurisdictional cooperation will be necessary for any sound management approach. Should cooperation not occur, the Councils are prepared to make a concerted effort to remove the exemption of highly migratory tuna from the Act, in order that large pelagic fisheries may be properly managed.

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Fishery Models as Applied to Elasmobranch Fisheries

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ABSTRACT

Some elasmobranch stocks have collapsed following a relatively brief period of exploitation. Descriptions of such collapses are provided for porbeagle shark fisheries in the Northwest Atlantic, the California soupfin shark fishery, the Australian school shark fishery, and the Scottish–Norwegian and British Columbia spiny dogfish fisheries. Life history characteristics and biological parameters of elasmobranchs are compared to those of teleosts. Previous attempts to assess elasmobranch stocks/fisheries are reviewed for the Scottish–Norwegian and British Columbia spiny dogfish, large sharks in the Western North Atlantic, elasmobranchs in the Gulf of Mexico, and kitefin sharks in the Azores. Several of these attempts employed stock-production models, but the most appropriate attempt was that on British Columbia spiny dogfish, which employed a deterministic age-structure model using data on growth, maturity, and fecundity. Some suggested approaches to assessing elasmobranchs using biomass (stock-production) and age-structured models, such as those used for marine mammals, are presented, with particular emphasis on data requirements. Stock-production models can provide estimates of MSY, but are more applicable for use with elasmobranchs when they are age-structured and account for a time delay between spawning and recruitment. Age-structure models can provide more realistic assessments and detailed forecasts. The principal obstacle to further progress in assessing elasmobranchs is the lack of appropriate data.

Introduction

Elasmobranchs have been exploited by fisheries in many parts of the world. In some cases, this exploitation has been caused by fisheries directed towards a particular species, whereas in other cases, elasmobranchs have been taken as bycatch in fisheries directed towards other species. Fisheries directed towards individual elasmobranch species, at least those that have expanded rapidly and become rather intense, have generally collapsed or declined markedly within a short period of time. Some attempts have been made to assess the impact of fishing activities on elasmobranch stocks or to estimate their potential yield. Most of these attempts have produced either uncertain results owing to insufficient data and/or the use of inappropriate models, or untested results due to nonimplementation.

Few elasmobranch stocks or fisheries have ever been regulated by any type of management scheme. They have a low market value. Data on catches/landings have been inadequate to evaluate the impact of fishing. Biological information such as growth rates, natural mortality rates, age composition, and stock identity has been insufficient. Scientific research (collection of basic biological information and development of appropriate assessment models) has been inadequate relative to that required for proper assessment and management. Public and governmental attitudes towards sharks, at least in most Western cultures, have not mandated conservation measures because of a lack of interest, low priority, perceived notions of inexhaustible shark resources, dislike for sharks, and so on.

The purpose of this paper is to review documented responses of elasmobranch resources to fishing activities, to contrast teleost and elasmobranch life history characteristics and biological parameters, to summarize past attempts to assess elasmobranch stocks and fisheries, and to suggest possible approaches for future assessments including data requirements.

Review of Past Fisheries Where Collapses Have Occurred

Porbeagle Fisheries in the Northwest Atlantic

Norway initiated a fishery for porbeagle sharks (*Lamna nasus*) in 1961 which ranged from the Newfoundland Grand Banks to waters off the Mid-Atlantic states of the east coast of the United States. Catches (by longline) increased from 1,824 tonnes (t) in 1961 to 8,060 t in 1964 but then declined to only 270 t in 1968. Catch per unit effort (CPUE) was 9.1 sharks/100 hooks in 1961 when the fishery began but dropped to only 2.9 in 1964 (S. Myklevoll, Institute of Marine Research, P.O. Box 1870, 5011 Bergen-Nordnes, Norway, pers. commun., November 1978), and presumably further in subsequent years. The Norwegian fishery lasted only six years (1961–1966), with small catches reported in 1968 and 1972.

A Faroese fishery began in 1964–1965 in generally the same area as the Norwegian fishery. It similarly experienced a drastic decline in CPUE within a few years and also a proportionate decrease in the average size of fish caught (K. Hoydal, Fiskirannsòknarstovan, Debessartrød, 3800 Tòrshavn, Faroe Islands, pers. commun., November 1978). In contrast to the Norwegian fishery, however, the Faroese fishery has persisted until the present time, but with relatively low catches that averaged only 360 t per year during 1964–1986.

California Soupfin Shark Fishery

Total California shark landings, of which soupfins, *Galeorhinus zyopterus*, were a high percentage, were fairly steady during 1930–1936 at an annual average of about 270 t, supplying a limited market for fresh shark fillets and fish meal and oil (Ripley 1946). However, a new market developed in 1937 following the discovery that the liver of the soupfin shark was the richest source of high-potency vitamin A available in commercial quantities. This discovery, together with sharp reductions in other sources of supply due to World War II, led to a tremendous increase in the fishery. Landings reached a peak of 4,185 t in 1939 but dropped sharply to 1,178 t in 1944. Landings recorded specifically as soupfin declined from 2,172 t in 1941 to 287 t in 1944. CPUE in the Eureka region declined from 55.4 fish/1,000 fathoms of gill net fished for 20 hours in 1942 to only 1.4 fish in 1944. It is assumed that CPUE must have been much higher than 55.4 in 1938 when the fishery first expanded, but that it underwent a very dramatic decline during 1938–1944 corresponding to an equivalent drop in shark abundance.

Australian School Shark Fishery

Total catches of school sharks, *Galeorhinus australis*, in southeastern Australian waters increased from 4 t in 1927 to a high of 1,639 t in 1949 before declining (Olsen 1959). The 1956 catch was 750 t. This expansion was due to a growing demand for fresh shark flesh and vitamin A (from the liver). CPUE declined from 13.7 sharks/100 hooks in 1944 to 7.3 in 1956.

Scottish-Norwegian Spiny Dogfish Fishery

A fishery for spiny dogfish, *Squalus acanthias*, has been conducted by trawlers in the northern part of the North Sea from the Norwegian coast to the area west of the Shetland, Orkney, and Hebridean Islands north and west of Scotland. Following World War II, landings from ICES Subarea IV and Division VIa rose from 6,600 t in 1946 to a high of about 37,200 t in 1958. There was a gradual decline in landings from then until 1986 (13,500 t). Holden (1968) noted that the catch rate by Grimsby trawlers of fish less than 55 cm total length fell from an average of 408 per 100 hours trawling during 1960–1962 to an average of 36 during 1968–1970.

British Columbia Spiny Dogfish Fishery

Catches in the British Columbia spiny dogfish fishery averaged less than 800 t/year during the 30-year period before the fishery began to intensify in 1937 in response to a demand for shark livers. Catches peaked at over 30,000 t in 1943, but fell to 2,000–3,000 t in 1949 (Wood et al. 1979). The fishable biomass was reduced to about 25% of its original size by 1948 (Ketchen 1969). The stock was not able to sustain a fishery that averaged 15,000 t/ year over a period of 13 years.

Basking Shark Fisheries

There have been periodic fisheries for basking sharks, *Cetorhinus maximus*, in coastal areas of the Northeast Atlantic and in the Western and Eastern Pacific. This species is especially vulnerable to harpoon fisheries, which has resulted in its rather rapid depletion in areas where it has been the focus of a fishery (e.g., Parker and Stott 1965).

Life-History Characteristics and Biological Parameters

Growth Rate

Age and growth determination is more difficult for elasmobranchs than for teleosts owing to the absence of bony parts or otoliths in the former. Nevertheless, age and growth parameters have been determined for many elasmobranchs using spines and vertebrae. Holden (1974) presented a method for estimating K, the von Bertalanffy growth coefficient, using length of the gestation period, length at birth, and maximum observed length. Based on available age and growth studies, growth is much slower in elasmobranchs than in teleosts, thus resulting in lower values of K.

Table 1.
Estimates of instantaneous natural mortality (M) and maximum age (T_{max}) in years for various elasmobranch and teleost species.

Species	Common name	Location	Reference[a]	M	T_{max}[b]
Cetorhinus maximus	Basking shark	Northeast Atlantic	1	0.046	31
Squalus acanthias	Spiny dogfish	British Columbia	2,3	0.094	70
Lamna nasus	Porbeagle	Northwest Atlantic	4	0.18	30
Sebastes marinus	Redfish	Gulf of Maine	5	0.10	50
Clupea harengus	Atlantic herring	Norwegian Sea	6,7	0.13	23
Gadus morhua	Atlantic cod	North Sea	8	0.20	13
Merluccius bilinearis	Silver hake	Scotian Shelf	9,10	0.40	9
Mallotus villosus	Capelin	East Greenland-Iceland	7	0.42	6
Ammodytes marinus	Sandeel	North Sea	11	0.60	6
Trisopterus esmarkii	Norway pout	North Sea	11	1.60	4

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[a] References: 1—Pauly (1978), 2—Wood et al. (1979), 3—McFarlane and Beamish (1987), 4—Aasen (1963), 5—Mayo (1980), 6—Dragesund et al. (1980), 7—Anonymous (1989), 8—Anonymous (1988a), 9—Terré and Mari (1978), 10—Fanning et al. (1987), 11—Anonymous (1988b).

[b] Some of the ages indicated refer to the plus-group used in assessment analyses and the actual observed maximum age might be higher.

Life Span

Age determination is uncertain for many elasmobranch species, but available age analysis indicates that they generally live much longer than teleosts (Cailliet 1989). Some spiny dogfish have been aged as old as 70 years (McFarlane and Beamish 1987).

Natural Mortality

Natural mortality rate and life span are inversely proportional. Species with long life spans have low natural mortality rates and vice versa. Consequently, elasmobranchs, as a general rule, have lower natural mortality rates than most teleosts (Table 1).

Maturity

Sexual maturity occurs as early as the first or second year for some fast-growing teleost species such as capelin, *Mallotus villosus*, or may begin at ages 8–9 and not be complete until about age 15 for slow-growing teleosts such as redfish, *Sebastes* spp. For most commercially-exploited teleosts in temperate waters, sexual maturity begins at about ages 2–3 and is fully achieved by about ages 5–6.

For elasmobranchs, there is uncertainty for some species in the age of maturation because of difficulties in age determination. However, available estimates are typically in the range of 2–8 years for many sharks, but higher for others (e.g., 25 years for dogfish).

Fecundity

Many elasmobranchs, particularly sharks, differ from most teleosts by being live bearers of their offspring. The number of young per litter for elasmobranchs is low, ranging from several to perhaps 100. In contrast, teleost females release larger numbers of eggs, ranging up to several million for cod or halibut. Survival of teleost eggs and larvae is very, very low, whereas that of the elasmobranch young is comparatively much higher. The gestation period for some elasmobranchs may last several years, whereas teleosts generally spawn annually.

Stock-Recruitment Relationship

There are density-dependent mechanisms which permit a teleost stock to alter its reproductive rate in response to changes in the size of its spawning component. The rate will approach zero in a very small stock biomass and increase as the stock increases. There are two general theories as to the response of recruitment to increases in spawning stock. The Ricker (1954) concept suggests a dome-shaped relationship in which recruitment reaches a maximum at intermediate levels of stock size and declines thereafter as stock size continues to increase. The Beverton and Holt (1957) model suggests that recruitment does not decline as stock size increases beyond intermediate levels, but tends toward an asymptotic limit (Fig. 1). As a teleost stock is subjected to fishing, it compensates by changing its reproductive rate by one or other of the above stock-recruitment theories.

Recruitment exhibits wide short-term variability for virtually all exploited teleost stocks (Hennemuth et al. 1980; Rothschild 1986). This is due primarily to environmentally-induced density-independent changes in the survival of the eggs and larvae. The extent to which recruitment is also directly dependent on the size of the parent spawning stock is likewise important. Because of the complexity of the biological processes involved and the extent to which random variability in recruitment is density independent, the

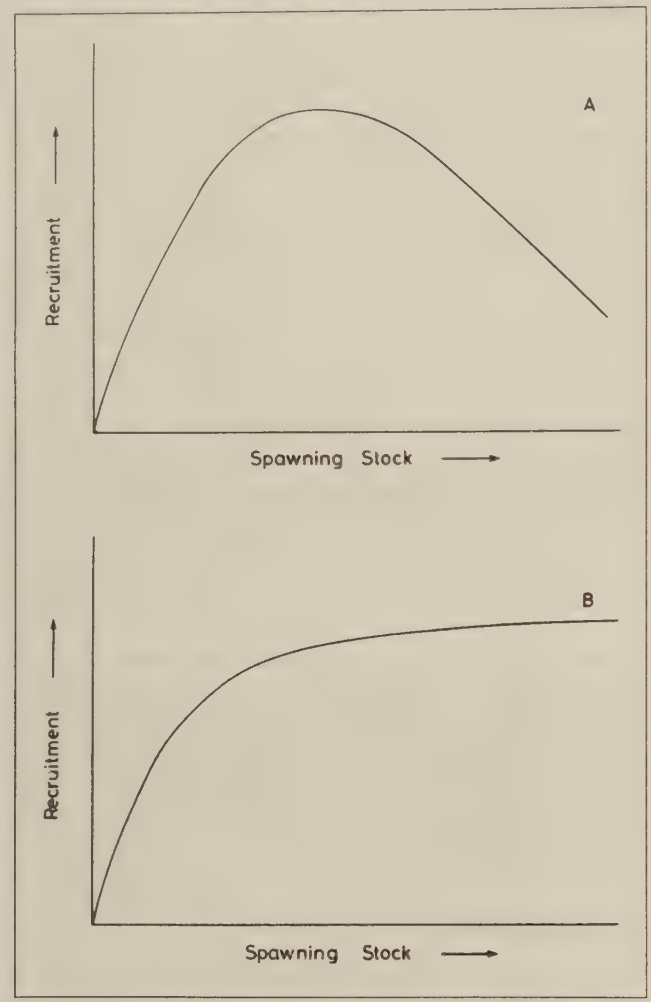

Figure 1.
Examples of stock-recruitment curves based on the Ricker (1954) model (A) and the Beverton and Holt (1957) model (B).

relationship between stock and recruitment is very difficult to determine and is not known with any degree of certainty for most exploited teleost stocks.

Given their low fecundity, the reproductive potential of elasmobranchs would appear to be greatest at or near the virgin level of spawning stock biomass and to decrease as the stock decreases. However, if they possessed absolutely no means of compensating for reductions in their populations, they would simply become extinct under exploitation. Density-independent factors are probably not very important in regulating stock abundance of elasmobranchs (e.g., Holden [1973] in the case of dogfish). Wood et al. (1979) suggested that compensatory change in natural mortality is the principal factor in the stock-recruitment relationship of British Columbia spiny dogfish. Holden (1973) felt that a density-dependent change in fecundity was the compensating factor for the Scottish-Norwegian dogfish stock. However, there seems to be evidence that dogfish stocks in different areas have dissimilar growth and fecundity rates.

Past Attempts at Assessing Elasmobranch Stocks/Fisheries

Scottish-Norwegian Spiny Dogfish

Holden (1968) assessed the effect of fishing on the Scottish-Norwegian stock of spiny dogfish and showed that the females must be protected to avoid an adverse effect on recruitment. Based on a relationship between the mean length at entry into the fishery and the instantaneous total mortality rate (Z) for constant recruitment, he demonstrated that the exploitation rate at that time was much greater than the stock could withstand.

Holden (1974) offered a method of quickly assessing the ability of an elasmobranch species to withstand exploitation. He proposed a general formula for the relationship between the annual rate of production of young and the Z at which constant recruitment will be maintained:

$$Z' = xe^{-Z't_m}, \tag{1}$$

where x = average number of female young produced per female per year and t_m = age at 50% maturity. He noted that this estimate of Z would, however, be the average for the whole life span and would not be applicable just to the exploited portion of the stock, but would likely be higher on prerecruits. Using this method, Holden (1974) estimated $Z = 0.22$ for Scottish-Norwegian dogfish and $Z = 0.8$ for an oviparous ray (*Raja* sp).

Holden concluded that, when elasmobranch young reach fishable size, the number of female fish in the population will only be sufficient to provide constant recruitment, and that sustained fishing on females will reduce the population considerably. He suggested that if there is an inverse relationship between growth rate and population density, growth will increase as a stock is exploited and its abundance begins to decrease, thus resulting in increased fecundity.

Large Sharks in the Western North Atlantic

Otto et al. (1977) attempted to estimate the maximum sustainable yield (MSY) for sharks (excluding dogfish) in FAO Areas 21 and 31 (Fig. 2). Using a Schaefer (1954, 1957) stock-production model with international commercial catch figures reported to FAO, U.S. recreational catch estimates, and CPUE from Japanese longline data for 1965–1974, they obtained an estimate of 41,000 t. This MSY estimate was used in the U.S. Department of Commerce Preliminary Fishery Management Plan for Atlantic Billfishes and Sharks which was drafted in 1977. It was

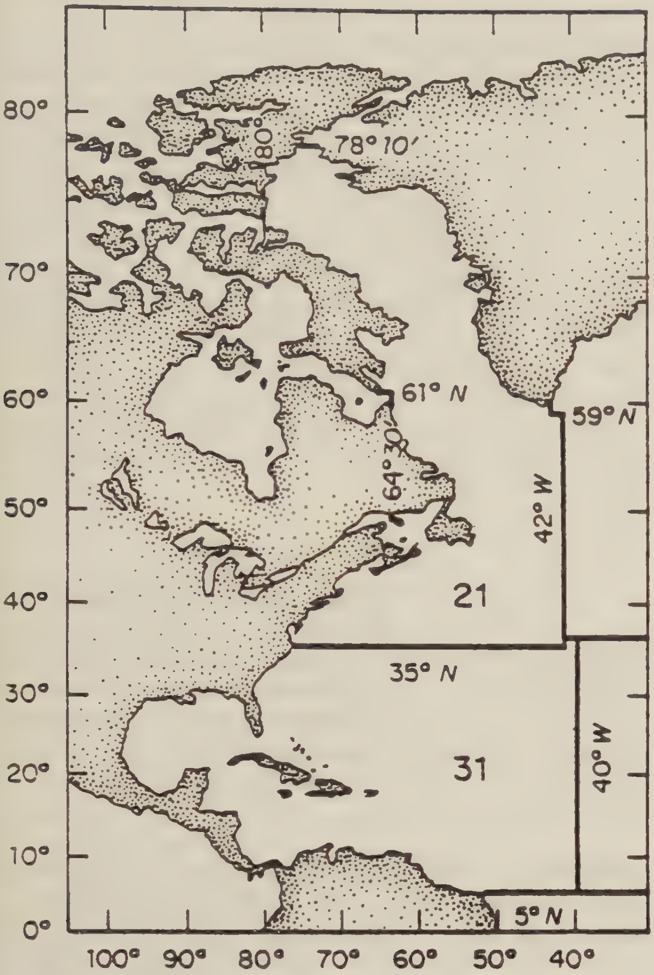

Figure 2.
Map showing FAO Areas 21 and 31 in the Western North Atlantic.

later determined (Anderson 1980, 1985) that the commercial catch data used by Otto et al. (1977) were grossly in error. Dogfish catches had inadvertently been included in the FAO Area 21 statistics as a result of U.S.S.R. dogfish catches having been reported as shark catches.

Anderson (1980) recalculated the MSY for sharks in the same area with revised catch data and Japanese CPUE from a slightly longer time period (1965–1977). The revised catch data included corrected international reported catches, estimated unreported catches, and estimated U.S. recreational catches. Annual CPUE was divided into the total estimated catch to obtain an estimate of international fishing effort expressed as an equivalent number of Japanese hooks fished. The generalized stock-production model of Pella and Tomlinson (1969) was fitted to the CPUE and the weighted average fishing effort using the method developed by Fox (1975):

$$U_i = (a + bf_i)^{\frac{1}{m-1}}, \qquad (2)$$

where U_i is the CPUE in year i, f_i is the weighted average fishing effort in year i, and a, b, and m are parameters which are estimated. Equilibrium conditions were approximated by averaging f over the number of years that a year class contributes significantly to the fishery. Gulland (1961) defined this as the mean life expectancy of a fish in the exploited stock, or $1/Z$. Gulland (1969) suggested that this number should be equivalent to half of the age span of the species in the exploited phase of the fishery. The average Z for 17 shark species considered by Anderson (1980) was 0.46. The reciprocal 2.17, rounded up to 3, corresponds to an age span of 6 years in the fishery. The model converged to a minimum residual sum of squares at $m = 1.65$, whereas a Schaefer logistic model would have an m of 2. The MSY estimated from this analysis was 25,700 t (Fig. 3). Other averaging periods were used, but 3 years gave the best fit.

The results of this analysis are largely uncertain because of questionable catch data, effort data from a fishery directed towards other species (tuna), and violation of the assumption of a unit stock (multiple species were represented in the catch data, and FAO Areas 21 and 31 do not necessarily represent the stock area for the various species considered). In the data series used, there were few catches that had effort values in excess of that which corresponded to the MSY estimate.

British Columbia Spiny Dogfish

Wood et al. (1979) developed a deterministic age-structure model which used data on growth, maturity, and fecundity to investigate the dynamics of spiny dogfish in British Columbia waters. This type of model, used widely for mammals, incorporates parameters of age-specific survival and reproduction. Equations were developed to estimate reproductive potential and instantaneous natural mortality (M). Density-dependent mortality, fecundity, and growth were evaluated for their ability to predict observed patterns in the historical fishery.

An estimate of $M = 0.094$ was determined for the equilibrium population. Simulations assuming compensatory mortality successfully predicted an anomalous age composition for 1978, trends in estimates of average litter size, and the unexpected increase in abundance of the stock about ten years after it had collapsed following intensive fishing. Since simulations assuming compensatory growth were not successful in predicting these events, Wood et al. (1979) concluded that compensatory change in M is the principal mechanism for density dependence in the stock.

Wood et al. (1979) obtained an estimate of MSY based on the following relationship proposed by Gulland (1970):

$$\text{MSY} \approx X \cdot M \cdot B_0, \qquad (3)$$

where B_0 is the virgin exploitable biomass, M is the

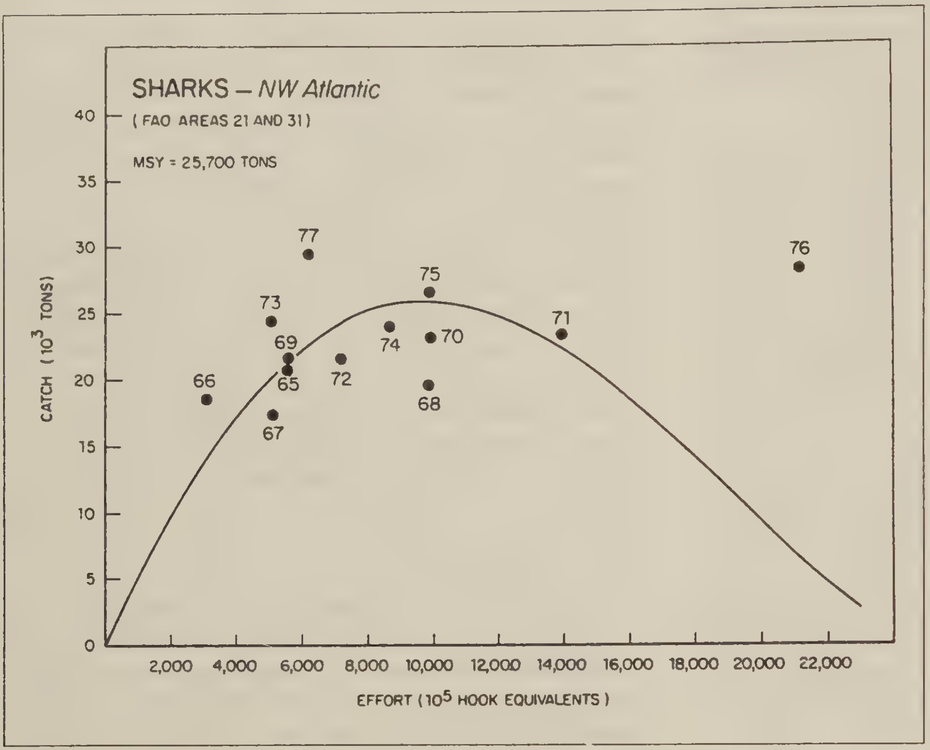

Figure 3.
Equilibrium relationship between catch and fishing effort for pelagic sharks in the Western North Atlantic using a 3-year weighted averaging period for effort. Actual data points are plotted (Anderson 1980).

natural mortality rate, and X is the maximum fraction that can be caught from the biological production of the stock, equal to 0.5 in the Schaefer stock-production model. Virgin biomass of the British Columbia dogfish stock was estimated to be about 200,000 t, using catch and effort data from the fishery conducted in the 1940s. Simulations indicated that MSY is attained when the marketable biomass has been reduced to 57% of its virgin level. Equation (3) can be expanded to:

$$X = \frac{F_{opt}}{M} \cdot \frac{B_{opt}}{B_0}, \qquad (4)$$

where F_{opt} and B_{opt} are the instantaneous fishing mortality rate and marketable biomass, respectively, at MSY. Assuming $M = 0.09$, $B_{opt}/B_0 = 0.57$, and $F_{opt} \approx M$ (i.e., 0.08–0.10), then MSY = 9,000–11,000 t.

Using their age-structure model with density-dependent M to project possible management implications, Wood et al. (1979) found no biological basis for a minimum size limit, and concluded that better stability in the fishery could be achieved by regulating F instead of catch.

Gulf of Mexico Management Plan for Sharks and Other Elasmobranchs

From the late 1970s to early 1980s, the Gulf of Mexico Fishery Management Council attempted to prepare and implement a fishery management plan for sharks and other elasmobranchs in the Gulf of Mexico. As a basis for establishing levels of optimum yield for different species groups, estimates of MSY were determined using estimates of standing stock biomass obtained from earlier exploratory longline research fishing surveys (GMFMC 1980). MSY was linked to these biomass estimates on the basis of equation (3). Since there had been very little fishing pressure on these species at the time of the longline surveys, the biomass estimates were assumed to be of virgin stocks.

In the Schaefer stock-production model, the relationship in equation (3) requires that $X = 0.5$ (MSY occurs when the stock biomass is reduced to 50% of its virgin level) and $F = M$. However, computations incorporating likely stock-recruitment relationships for elasmobranchs were made suggesting that stock biomass at MSY will be significantly less than half the virgin level. It was shown that a relationship between MSY and virgin biomass, depending on the growth coefficient K, M, and the age or relative length at recruitment, could be derived. Holden's (1974) method was used to estimate K, Z, and M for the major shark species found in the Gulf. Assuming the ratio of length at recruitment vs. L_∞ to be 0.5, MSY/virgin biomass = $M/4$, which is half the amount assumed by the Schaefer model. The F associated with MSY under these conditions is $0.65M$. Assuming $M = 0.3$ for most Gulf sharks, MSY would be 0.075 times virgin biomass. The associated F at MSY would be 0.195 (i.e., 0.3 × 0.65), and the biomass at MSY would be 0.075/0.195 or 0.385 times virgin biomass.

Based on these numerical relationships, the following MSY estimates were determined for various groups of shark species in the Gulf: large inshore/shelf sharks = 12.0 million lb (5,443 t), small inshore/shelf sharks = 18.0 million lb (8,165 t), large offshore sharks = 2.9 million lb (1,315 t), small offshore sharks = 4.3 million lb (1,950 t), and skates, rays, and miscellaneous elasmobranchs = 10.0 million lb (4,536 t). The scientific basis for these estimates was not accepted in the review of the proposed plan. Many of the biological parameter estimates used in the analysis were considered to be inappropriate (e.g., $M = 0.3$ was considered to be too high for long-lived species such as sharks). The management plan, therefore, was not adopted and implemented.

Kitefin Sharks in the Azores

The kitefin shark, *Dalatias licha*, is one of the most important demersal species in the commercial fishery in the Azores (Silva 1983). It is fished mainly with handlines from small boats, but in recent years, fishing has also been by larger boats using bottom nets. Catches peaked at about 950 t in 1981 and averaged 810 t annually during 1984–1986 (Silva 1987).

Silva (1983) obtained a preliminary estimate of MSY of 579 t for the stock by applying a Schaefer stock-production model to catch and handline effort data for the period 1977–1981.

Silva (1987) applied Fox's (1970) exponential surplus-yield model to a longer time series (1972–1986) of catch and effort (longline and bottom net) data, treating males and females both separately and in combination. The years 1972–1976, characterized by a constantly increasing catch per unit effort (CPUE), were considered to be a learning period and were excluded from the analysis. Results indicated an annual MSY of 933 t corresponding to 294 effort units for sexes combined, 666 t and 283 effort units for males, and 270 t and 320 effort units for females (Fig. 4). The MSY effort level for the combined sexes corresponded to 12,200 man trips fishing with handlines or to 294 days fishing with bottom nets. Since exclusive application of either mode of effort would result in overexploitation of one of the sexes, an optimum mixed solution was determined which corresponded to 281 days of fishing with bottom nets and 359 man trips fishing with handlines.

This application of a stock-production model appears to be valid in that there is a well-defined directed fishery for the species in question and there is a strong likelihood that a unit stock is being considered. However, the relatively short time series of catch and effort data (1977–1986) is probably insufficient to reflect properly the full response of the stock to fishing.

Possible Approaches for Assessing Elasmobranchs

Many of the previous attempts at assessing elasmobranch stocks, particularly sharks, have produced questionable results owing to insufficient data or the use of inappropriate models. While some types of models developed for assessing teleost stocks may be equally applicable to some elasmobranch stocks, assuming the availability of suitable data, others may not be appropriate in view of the marked differences in some biological parameters between teleosts and elasmobranchs, particularly reproductive potential. Biological processes such as growth and reproduction are considered only implicitly in some fishery models (e.g., stock-production). Consequently, it is necessary both to consider the types of existing teleost models that can perhaps be used to assess elasmobranchs and also to draw attention to assessment models developed for other animals (e.g., marine mammals) that might be more appropriate. Regardless of the type of model used, reliable data are necessary.

Assessment models can be classified into two general categories: biomass models and age-structure models.

Biomass models (e.g., stock-production) are able to provide a very general description of the status of a stock, particularly its MSY. Such models are especially useful during the early stages of an assessment when data for a more complete and descriptive assessment are lacking. They can be employed to make specific predictions (e.g., MSY), but are useful to only a limited extent and then need to be replaced by more detailed models. Certain complex features of biological systems can be incorporated into biomass models (e.g., time lags and natural variability in the response of the system to perturbations), but important aspects of the biological structure of a stock are ignored, and constitute a major weakness of these models. Detailed descriptions of a stock (e.g., past and present size by age group, year-class strength, history of fishing mortality rates by age, etc.) and predictions of its size and response to changes in its structure and the fishery on it can only be tested in a very general way.

Age-structure models that permit distinctions to be made between the age and/or sex of individuals in the stock, are consequently more realistic, and allow more detailed predictions to be made. However, this type of model requires more data, which is its main limitation. Sampling of biological information must be done carefully and on a random basis. Age-structure models can guide research efforts by indicating those parameters whose estimation is most important in understanding the dynamics of the stock. The degree of importance of particular parameters will depend on fishing strategies or management actions. Simulations of different fishing strategies (e.g., size of fish at capture,

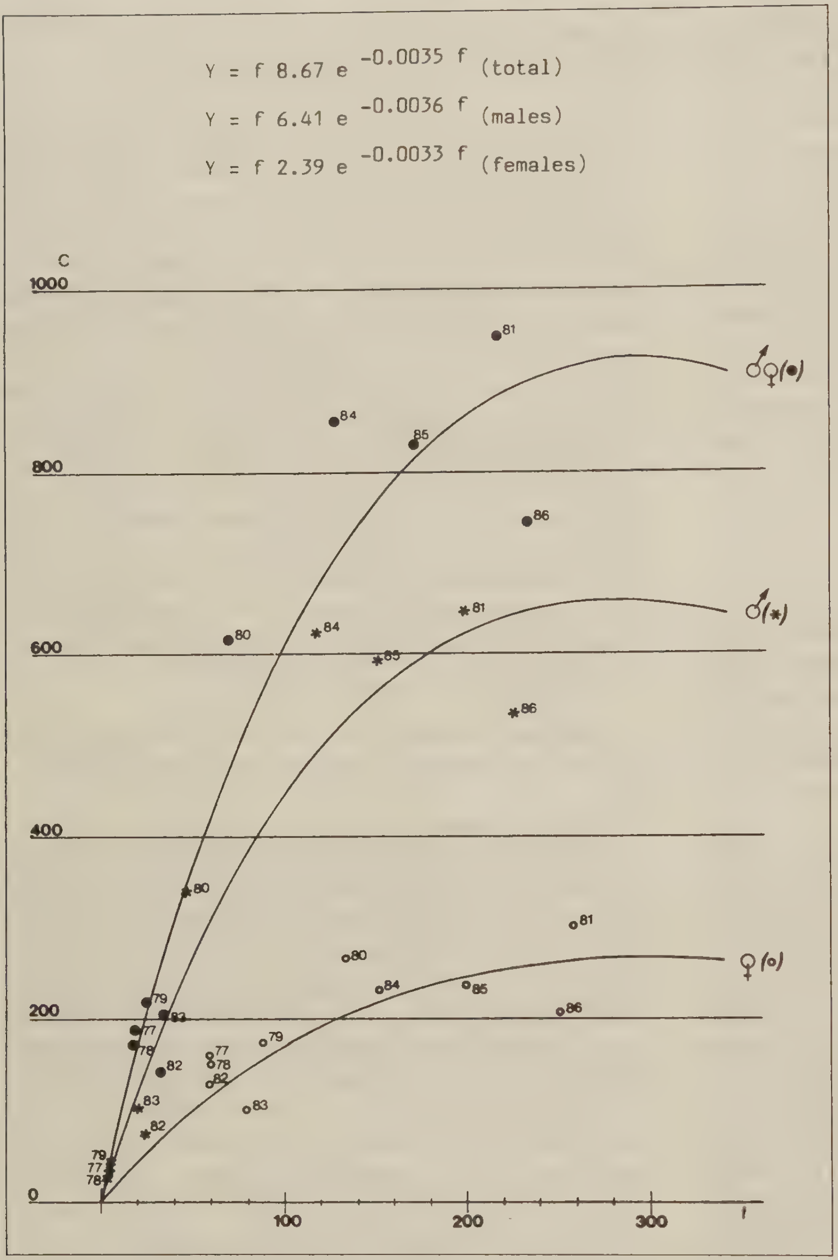

Figure 4.
Equilibrium relationships between catch and effort for the Azores kitefin shark fishery for sexes combined and separated based on Fox's (1970) exponential surplus yield model (Silva 1987).

level of fishing effort, annual catch level, etc.) can be accomplished.

Biomass or stock-production models should be valid for elasmobranchs providing that adequate input data (e.g., catch and CPUE or effort data) are available for the stock in question. If the data series is of sufficiently long duration, the response of the stock to fishing will be reflected in these parameters. An appropriate stock-production model [there are many that have been developed, such as those by Schaefer (1954, 1957), Pella and Tomlinson (1969), Fox (1970), Walter (1973), Deriso (1980), and Schnute (1985)] could then be fitted to the data to estimate the MSY level and the corresponding stock size (in a relative sense if only CPUE data were available or in an absolute sense if stock size estimates were available). Most of these models are not age-structured and provide little, if any, insight concerning the dynamics of the stock (Anonymous 1987). However, models such as those by Deriso (1980) and Schnute (1985) are age-structured and account for a time delay between spawning and recruitment. Since such a delay for sharks could easily be 10–20 years, this type of stock-production model would be more appropriate for sharks.

Some of the models developed and used in assessing marine mammals (FAO/ACMRR 1978, 1981; Fowler and Smith 1981) were based on models used for terrestrial mammals and may also be applicable to sharks by virtue of the similarity between the two groups of animals, e.g., low fecundity/litter size, slow growth and long life span, and close relationship between stock and recruitment. The development of whale stock models has been based on techniques and concepts used in modeling both fish and mammal stocks (Allen 1981). The first models employed simple techniques developed in studying fish and could be applied where little biological data were available. These models initially accomplished little more than providing estimates of MSY, but later became more complex in order to simulate more closely the internal dynamics and external relationships of the stocks. They are age- and frequently sex-specific, include estimates of recruitment and natural mortality, and incorporate time lags (all of which require knowledge of when sexual maturity and full vulnerability to fishing occurs). The models must be capable of estimating MSY and the corresponding stock size as well as yield at alternative stock levels. The age-structure models require extensive data on fecundity rates/litter sizes and growth and natural mortality rates by age and sex, preferably at variable stock levels to determine the extent of density dependence or independence.

To the extent that appropriate data exist for shark species stocks, age-structure models could be developed to simulate their dynamics. Unfortunately, as indicated earlier, little work has been done to date. The model developed by Wood et al. (1979) for the British Columbia spiny dogfish stock is about the only example of an age-structure model successfully applied to elasmobranchs. Further efforts along this line should be encouraged.

The lack of model development on shark stocks has resulted in an absence of firm evidence on the effect of stock reduction by fishing on parameters such as growth, *M*, and recruitment. As indicated earlier, Wood et al. (1979) concluded from their model that *M* was the density-dependent factor that best explained changes in that stock. However, substantial changes in recruitment rates are believed to occur with changes in whale stock abundance (FAO/ACMRR 1978). Adjustments to this parameter, rather than to *M*, in the whale models are mainly responsible for differences in sustainable yields at different stock levels. Further investigation is necessary to determine if changes in stock levels influence the same biological parameters in both sharks and whales.

From the limited number of shark MSY estimates described in this paper for which corresponding estimates of relative or actual stock biomass are available, a comparison can be made between whales and sharks with respect to the relationship between MSY and virgin biomass (i.e., the stock biomass level at which MSY occurs relative to the virgin biomass level, and the magnitude of MSY expressed as a percentage of the virgin biomass level). The MSY levels for large mammals in general occur well above 50% of their virgin biomass level (Fowler 1981). Most models now used as a basis for management within the International Whaling Commission assume that MSY occurs at 60% of the virgin biomass level (Allen 1981). For southern minke whales, MSY has been estimated to occur at 53% of the virgin stock size and to be equivalent to 4.1% of the virgin stock (Gambell 1981).

Wood et al. (1979) estimated MSY for British Columbia spiny dogfish to occur at 57% of the virgin stock level and to be equivalent to 4.5–5.5% of the virgin biomass. These values are consistent with those indicated above for whales.

On the other hand, the MSY estimate for large sharks in the western North Atlantic by Anderson (1980) occurs at 48% of the virgin biomass level, and the stock level at which MSY occurs for kitefin sharks in the Azores (Silva 1987) corresponds to 35% of the virgin level. Data on the absolute levels of virgin biomass were not available for either of these analyses to ascertain the size of the MSY estimate as a percentage of virgin stock biomass. The formulae developed for estimating MSY levels for shark groups in the Gulf of Mexico (GMFMC 1980) suggested that MSY would be 7.5% of the virgin biomass and would occur at 38.5% of the virgin level. These estimates are not in agreement with those for whales or those determined by Wood et al. (1979), and may reflect the use of models inappropriate for sharks or incorrect data. Based on what is known about shark reproduction, it would be prudent to assume that MSY should occur at levels of stock biomass closer to the virgin level than the 35–48% levels suggested above. Further research is needed to clarify this possibility.

One of the most commonly used analytical techniques for assessing commercially exploited marine teleost stocks is virtual population analysis (VPA) (Gulland 1965) or cohort analysis (Pope 1972). In theory, this method could also be employed to assess the status of shark or other elasmobranch stocks if the appropriate data were available. VPA can be used when a time series of catch-in-number-at-age data exists. Given an estimate of *M* at each age throughout the time series and *F* at each age in the latest year, the method performs an iterative computational procedure back in time to produce estimates of stock size (including recruitment) in number and *F* at each age in all years. The stock size at age in the latest year can be used as a basis for forecasting both catches and resulting stock sizes. The ability to produce reliable forecasts is dependent upon the accuracy of the stock size estimate (or the estimated *F* at age) in the latest year and the estimates of recruitment in the forecast years.

Data requirements for performing adequate assessments on elasmobranch resources include the following:

Catch Statistics—Accurate figures are required on the catch of each species in directed fisheries, as well as on bycatch in fisheries directed towards other species (e.g., longline fisheries for swordfish, tuna, etc.). Catch statistics must be available by species, area, and (if necessary) by stocks.

CPUE or Effort Data—Catch per unit effort or fishing effort from directed fisheries for elasmobranchs must be reported. In cases where catches occur incidentally in fisheries directed towards other species, effort data for the main species should also be reported.

Sampling Data—Random samples must be taken from the landed catch to obtain length, weight, sex, age, and maturity data. If possible, sampling should also be done aboard vessels at sea to obtain comparable data on fish that are discarded. This information is needed to estimate the number of fish caught at each age (and sex, if necessary) and the proportion of mature fish at each age.

Stock Identification—Assessments have to be on a unit stock basis. It is necessary, therefore, for stock boundaries to be defined and for catches to be assigned to the appropriate stock.

Age and Growth Studies—Such research is necessary to provide the basis for determining the von Bertalanffy growth parameters that are required in certain assessment models and also for providing the routine ageing of fish sampled from commercial and research catches.

Natural Mortality—In order to account for natural deaths in an analytical assessment, the natural mortality rate must be estimated, preferably by age.

Recruitment—In order to make projections of stock size and potential catch, estimates must be made of the number of fish entering the exploited component of the population each year. In the case of elasmobranchs, where recruitment is not as variable as in teleost stocks, this could perhaps be estimated from the estimated number of mature females in the stock, the fecundity/litter size, and natural mortality rate in the prerecruit phase.

Fishery-Independent Data—Estimates of the size or relative size of the stock would be useful. Depending on the species involved, such estimates can be obtained from research vessel surveys using bottom trawls (e.g., for dogfish, skates and rays), longlines (e.g., large sharks), etc. Data collected from catches during such surveys should include length, weight, age, sex, and maturity.

Mark-and-Recapture Studies—This type of study can provide estimates of the exploitation rate of the stock, the size of the stock, the survival rate of the stock over a given time interval, and the rate of recruitment to the stock. A number of assumptions must be satisfied in order for the results from this type of study to be valid (Ricker 1975).

The extent to which such data are available, and their quality, will determine the type of assessment which is possible as well as its reliability. The biological and statistical material on which many of the data requirements are based must be obtained from research and/or fishing activities. This responsibility rests with relevant national governmental agencies. Assessment responsibilities reside with these same agencies and/or other national or international agencies or organizations mandated to manage the resource in question.

The principal obstacle at the present time to further progress in assessing the status of elasmobranch stocks is the lack of data. This shortcoming has discouraged the necessary development of models to properly assess these unique species. If significant progress is to be achieved, marked improvements must be made in the collection of data, particularly those from the fisheries. In the absence of badly needed progress both in data collection and model development, scientists will continue to make broad, weakly based generalizations about the likely impact of fishing activities on these stocks, and future attempts to manage elasmobranchs will have no sound scientific basis.

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The Skates and Rays of the Western North Pacific: An Overview of their Fisheries, Utilization, and Classification

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ABSTRACT

Since 1953, the annual catch of skates and rays in Japan has ranged from about six hundred to about nineteen hundred metric tons, but they are not caught in large numbers by Japanese trawlers. The nutritive value (contents of protein, lipid, and carbohydrates, etc., for example) of some skates and rays and their utilization by the Japanese food industries are reviewed. Seventeen families of the western north Pacific skates and rays are classified into three ranks (A, B, and C) according to the degree of development of their systematic characteristics. A list of the valid species of skates and rays in the area is made after a systematic discussion.

Introduction

For over two thousand years, the Japanese people have used fishes as their main source of protein. Presently, they land more fishes than any other country in the world (FAO 1986). Although the Japanese catch of elasmobranchs is approximately fourteen thousand metric tons, directed commercial fisheries for skates and rays do not exist in Japan. Recently, the annual incidental catch for batoids reached about ten thousand metric tons. Elasmobranchs are very susceptible to overfishing (Holden 1974) and stocks of skates have been overfished when they are target species (Brander 1981). The increased Japanese landings demonstrate a need for stock assessment and life history studies to permit an understanding of western North Pacific batoids and their rational exploitation.

This overview is a step toward understanding the Japanese resource of skates and rays; the Japanese fisheries that involve them; their utilization and nutritive value as food, and their classification.

Resources

Catch of Skates and Rays in Japanese Waters

Annual catch of skates and rays in Japan has been recorded from 1925 to the present, but an accurate data collection began only in 1953. The catch of skates and rays in Japan ranges from 6,424 t (in 1974) to 18,782 t (in 1955) (Table 1). The catch in the East China Sea has been recorded since 1947. More than half of the total catch of skates and rays in Japan has usually been taken in the East China Sea. Yamada (1986) stated that the catch of skate, families Rajidae and Pseudorajidae, reaches 3,700–4,700 t a year in the East China Sea, and that of the stingray, *Dasyatis akajei*, reaches 250 t. *Raja boesemani* is caught more than any other skate (2,500–3,100 t a year), followed by *Raja kwangtungensis* (1,200–1,600 t) (Yamada 1986). *Raja acutispina* is also commonly caught in the East China Sea. Although the catch of skates and rays amounts to less than 10,000 t a year in Japan, if a commercial fishery targets skates and rays, an increased catch is possible. At present, these batoids are a bycatch of other edible fishes and are usually returned to the sea. An exception is a trawler fishery in the East China Sea, which catches skates and rays almost exclusively, and another in Hokkaido, which catches *Raja pulchra* exclusively in winter.

At present there are no data available to assess the abundance of skates and rays in the western North Pacific. It is recommended that the studies of skates and rays, as a resource, be carried out in the near future.

Biological Studies on the Skates and Rays in the Western North Pacific

There have been only a few studies on the biology of skates and rays in the western North Pacific, partly because the classification is still poorly understood (see Classification

Table 1.
Annual catch of skates and rays in Japan since 1947. Data from the Statistics Information Center of the Fisheries Agency, Japan (1979); the Statistics Information Center of the Fisheries Agency, Japan (1963–1989)[a]; and the Fukuoka Office of the Fisheries Agency, Japan (1947–1966).

Year	Total	East China Sea	Sea of Japan	Hokkaido
1947	1,683	1,683	—	—
1948	1,731	1,731	—	—
1949	1,136	1,136	—	—
1950	701	701	—	—
1951	—	2,381	—	—
1952	—	10,519	—	—
1953	17,168	11,254	—	—
1954	18,469	12,814	—	—
1955	18,782	12,855	—	—
1956	18,070	11,618	—	—
1957	17,676	10,609	—	—
1958	16,783	10,404	—	—
1959	15,490	8,703	—	—
1960	14,202	8,772	—	—
1961	13,048	8,087	—	—
1962	12,403	7,291	—	—
1963	13,707	7,981	3,277	2,938
1964	12,148	7,287	2,900	2,100
1965	10,323	5,704	2,731	2,114
1966	10,732	5,682	2,707	2,588
1967	10,589	5,258	2,970	2,857
1968	—	4,974	—	—
1969	8,457	4,522	2,580	1,978
1970	10,161	5,948	2,518	2,495
1971	7,681	5,049	1,286	1,553
1972	6,963	4,827	1,342	1,129
1973	7,539	5,213	1,410	1,381
1974	6,424	4,406	929	1,029
1975	7,684	4,311	1,161	2,095
1976	7,819	4,154	1,140	2,336
1977	9,409	4,379	1,148	3,789
1978	8,264	4,893	875	2,096
1979	7,496	4,995	781	3,135
1980	11,884	5,338	696	5,181
1981	9,400	4,856	670	3,129
1982	9,990	4,717	514	3,798
1983	8,083	3,859	513	2,640
1984	9,065	4,166	335	3,268
1985	6,577	3,207	349	1,729
1986	6,610	3,010	407	2,053
1987	6,799	—	—	—
1988	6,637	2,523	387	2,890

[a] Data from some minor districts are omitted.

Table 2.
Food composition of skates and rays in the western North Pacific. Data for *Rhinobatos schlegelii* and *Platyrhina sinensis* after Koreeda et al. (1982). Data for *Raja kenojei* after the Resource Council, Science and Technology Agency, Japan (1982).

Food composition	*R. schlegelii*	*P. sinensis*	*R. kenojei*
Yield rate (%)	34.6	43.5	44.4–49.0
Energy (kJ)	—	—	255
Moisture (g)	75.7	76.0	84.7
Protein (g)	15.5	21.2	13.3
Lipid (g)	1.4	2.0	0.5
Carbohydrates (g)	—	—	0.1
Ash (g)	0.93	1.18	1.4

Table 3.
Composition of vitamins, minerals, and mercury in the muscle of a skate, *Raja kenojei*, and *Platyrhina sinensis*. Data for the skate after the Resource Council, Science and Technology Agency, Japan (1982) and the data for *Platyrhina sinensis* after Koreeda et al. (1982).

Food composition	*R. kenojei*	*P. sinensis*
Vitamin B_1 (mg)	0.05	—
Vitamin B_2 (mg)	0.12	—
Niacin (mg)	2.0	—
Ca (mg)	5	—
P (mg)	140	—
Fe (mg)	0.5	—
Na (mg)	310	—
K (mg)	130	—
Hg (ppm)	—	1.07

section) and because they are often considered to be inedible. Ishiyama (1951a, b; 1955) and Ishiyama and Okada (1955) published a theory of age determination, reproductive biology, age composition and growth rates of skates occurring in the East China Sea. Yokota (1951, 1952) reported the age composition of a stingray, *D. akajei*, caught off Totoro, Miyazaki Prefecture. Takemura (1987) reported the food habits of some skates in the East China Sea.

Utilization (Skates and Rays as Food)

Skates and rays are similar to bonyfishes or sharks in their nutritive value. In general, skates and rays are processed into fish meat jelly (Kamaboko) and dried skate wing (Ei-hire). The species of skates and rays used as food are indicated below.

Nutritive Value

Muscle—Food composition of a few skates and rays are shown in Tables 2 and 3. Yield rate varies from 34.6% (guitarfishes) to 49% (skates) (Shimizu 1934; Ohshima 1949; Koreeda et al. 1982). Moisture ranges from 75.7%

Table 4.
Comparison of sarcoplasmic protein, myofibrillar protein, and stroma protein in the muscle of skates and rays. Data for *Torpedo marmorata* after Bailey (1939); data for *Rhinobatos schlegelii* and *Platyrhina sinensis* after Koreeda et al. (1982).

Protein types	*T. marmorata*	*R. schlegelii*	*P. sinensis*
Sarcoplasmic protein (S.P.)	26 g/100 g	4.02 g/100 g	4.23 g/100 g
Myofibrillar protein (A.M.)	64 g/100 g	5.02 g/100 g	9.82 g/100 g
Stroma protein	10 g/100 g	—	—
A.M./S.P.	2.46	1.25	2.32

to 84.7% and is almost equal to that of bonyfishes as well as to sharks. The protein composition of some skates and rays are shown in Table 4. The rate of stroma protein in the muscle of elasmobranch fishes is high and thus the skin is full of collagen which is readily converted to gelatin. The amino-acid composition of muscle protein of skates, *Raja clavata* and *Raja montagui*, reported by Gerdy and Teuwis (1972) is shown in Table 5. Only a small amount of lipid is found in the muscle of skates and rays (see Table 2). Extractive components, such as nitrogen, affect the taste of fish muscle and are contained in the muscle of elasmobranch fishes in large amounts. Suyama et al. (1958) reported that in *D. akajei*, there are 3,035 mg% total nitrogen and that 1,281 mg% nonprotein nitrogen are present. Almost all the nonprotein nitrogen (extractive nitrogen) in the elasmobranch fishes are those of urea and TMAO (trimethylamine oxide). Urea and TMAO content in the muscle of certain rays reported by Suyama (1960) are shown in Table 6. Free amino-acid in skates and rays were reported by Boyd et al. (1977) for *Raja erinacea* and *D. sabina*. Vitamin content is very small in skates and rays (see Table 3). Yamakawa et al. (1965) reported that there is no vitamin D in the muscle of elasmobranchs, but that pro-Vitamin D is present in the muscle of skates and rays. Diplok and Haslewood (1967) reported that ubiquinone, which is a source of cellular activity, is also present in the muscle of *R. brachyura* and *T. nobiliana*. There are only a few minerals, such as Calcium, Phosphorus, Iron, Sodium, and Potassium in the muscle of skates and rays (see Table 3). It is noteworthy that a high average content of mercury (1.07%) was found in the muscle of *Platyrhina sinensis* (see also Table 3).

Table 5.
Amino acid composition of parvalbumins in the muscle of *Raja clavata* and *R. montagui* as reported by Gerdy and Teuwis (1972).

	R. clavata (g/100 g)	*R. montagui* (g/100 g)
Gly	8	7
Ala	12	12
Val	4	4
Leu	9	10
Ile	6	6
Ser	11	11
Thr	5	7
Met	2	1
Cys	2	2
Pro	1	1
Phe	8	8
Tyr	1	1
Try	0	0
Asp	16	17
Glu	10	8
NH_3	6	—
His	3	4
Lys	11	13
Arg	1	1

Table 6.
Distribution of urea and TMAO in fresh muscle samples of skates and rays. Data after Suyama (1960).

Species	Urea (mg%)	TMAO (mg%)
Raja boesemani	2,032–2,167	1,220–1,360
Dasyatis akajei	1,809–1,897	—
Urolophus aurantiacus	1,995	1,050
Mobula japonica	1,830	1,425

Liver Oils—Liver oils of skates and rays were investigated by M. Tsujimoto, who was the discoverer of squalene. Tsujimoto (1916, 1918, 1922, 1923, 1928, 1936), Tsujimoto and Kobayashi (1920) and Tsujimoto and Toyama (1922) found that griseril ether, such as selachil and bathyl alcohol, is present in the liver of skates and rays. Kaneda et al. (1955) studied the nutritive value of liver oils in marine animals and concluded that the liver oil of *Dasyatis akajei* had a high nutritive value.

Cost—As is shown in Table 7, skates and rays are still inexpensive, although the catch is small and processing is difficult. They may also remain as expensive as fishes and sharks in the future.

Food Technology of Skates and Rays

Fish Meat Jelly—Excepting the electric rays, fresh skates and rays are usually used to make fish meat jelly (Kamaboko). Shimizu et al. (1981) and Koreeda et al. (1982) investigated elasmobranch fishes to learn what species are

Table 7.
Wholesale price of skates and rays for the past ten years compared to sharks and codfishes, (yen/kg). Data from the Statistics Information Center of the Fisheries Agency, Japan 1987).

Year	Skates and rays	Sharks	Codfishes
1979	111	123	170
1980	114	132	202
1981	109	141	170
1982	125	170	154
1983	188	138	160
1984	120	143	185
1985	124	144	142
1986	193	157	130
1987	188	158	135
1988	175	139	143

suitable for fish meat jelly. They concluded that a fan ray (*P. sinensis*) and a stingray (*D. akajei*) were excellent but that the guitarfish (*Raja schlegelii*) was not suitable.

Dried Skate Wing—For dried skate wing (Ei-hire), both skate wings are cut off from the main body and dried. Dried wings are usually eaten with wine. In Nagasaki and Hokkaido, skates are usually processed into dried skate wing products.

Other Uses—In ancient times, the skin of skates and rays was used for the covering the handles of swords. Miwa (1980) reported that guitarfishes were eaten after steeping in boiling water (Yubiki). They are sometimes used for shark fin soup (Fukahire) and fishbones (Meikotsu). Some dasyatid stingrays are sometimes cooked as a main dish in restaurants featuring French cuisine.

Classification

The fauna of skates and rays in the western North Pacific includes seventeen families of the superorder Batoidea: Pristidae, Torpedinidae, Narcinidae, Narkidae, Rhinobatidae, Platyrhinidae, Rhynchobatidae, Rhinidae, Pseudorajidae, Rajidae, Dasyatididae, Gymnuridae, Urolophidae, Hexatrygonidae, Myliobatididae, Rhinopteridae, and Mobulidae. It lacks only two families, Hypnidae and Potamotrygonidae, of the superorder. The systematic study of the western North Pacific skates and rays is incomplete, not only because they are considered to have a low commercial merit (see Utilization section), but because their taxonomy is difficult to understand owing to ambiguous specific characters and insufficient information on morphological variation.

Based on the literature concerning the fauna of the western North Pacific skates and rays, and on examination of material archived in the Museum of the Tokyo University of Fisheries (MTUF), I attempted to provide an overview of their systematics, to clarify the many systematic problems that still exist in the western North Pacific skates and rays, and finally to present a check list of the valid species in this area (see Table 10). The literature used in the present study includes Annandale (1909, 1910); Garman (1913); Fowler (1941); Herre (1953); Matsubara (1955); Lindberg and Legeza (1959); Zhu (1960); Teng (1962); Fowler (1969a, b, 1970); Chen and Chung (1971); Gloerfelt-Tarp and Kailola (1984); Masuda et al. (1984); Monkolprasit (1984); and Shen (1984). Additional literature is included with each section of families. Although I follow the higher classification of the superorder Batoidea proposed by Nelson (1984), I have elevated some of his tribes and subfamilies to family rank. Also, the higher classification of the skates, suborder Rajoidei, follows McEachran (1984) and Ishihara and Ishiyama (1986), who considered that there are two families and 26 genera and subgenera in the suborder. Regarding the number of genera and species of each world-wide family, I agree with Nelson (1984), except for the number of skates, which is based on the unpublished data of McEachran (Texas A&M Univ., Texas, Oct. 1985), Stehmann (Institut für Seefischerei, Hamburg, Aug. 1987) and Ishihara. Also the number of genera and species of Dasyatididae follows mainly Fowler (1941, 1969a, b, 1970) (Table 8 for comparison between the number of skates and rays in the western north Pacific and in the world). The order of families follows Nelson (1984).

To clarify the understanding of the systematics of each family, I used the rankings proposed by Utinomi (1956), who classified the sea animals of Japan (39 groups) into five rankings, A to E. However, there are no western North Pacific skates and rays which belong to the ranks D and E (Table 9).

Pristidae

Two genera and four species have been recorded from the western North Pacific (Table 10). All four species appear to be valid and records of the species seem to be trustworthy. Gloerfelt-Tarp and Kailola (1984) stated that *Pristis microdon* Latham might be a junior synonym of an Atlantic species, *P. pristis* Linnaeus. This problem should be addressed based on a comparison of the species between the Atlantic and Indo-Pacific.

Torpedinidae

One species, *Torpedo tokionis* Tanaka, was described and is frequently recorded from Japanese waters. Recently, *T. californica* Ayres was recorded from the waters off northern

Table 8.
Number of genera (including subgenera) and species of western North Pacific skates and rays in each family. Number of those in the world are shown in parenthesis, after Nelson (1984).

Family	Genera	Species
1. Pristidae	2 (2)	4 (6)
2. Torpedinidae	1 (1)	2 (13)
3. Narcinidae	2 (4)	7 (15)
4. Narkidae	2 (4)	4 (9)
5. Rhinobatidae	1 (4)	6 (40)
6. Platyrhinidae	1 (3)	2 (5)
7. Rhynchobatidae	1 (1)	1 (2)
8. Rhinidae	1 (1)	1 (1)
9. Pseudorajidae	3 (7)[a]	25 (68)[a]
10. Rajidae	4 (19)[a]	17 (120)[a]
11. Dasyatididae	6 (6)	29 (60)[b]
12. Gymnuridae	2 (2)	4 (10)
13. Urolophidae	2 (2)	3 (30)
14. Hexatrygonidae	1 (1)	5 (1)
15. Myliobatididae	3 (4)	7 (24)
16. Rhinopteridae	1 (1)	3 (3)
17. Mobulidae	2 (2)	5 (10)
Total	35 (64)	125 (417)

[a] Ishihara, unpubl. data.
[b] Data from Fowler (1969a, b, 1970).

Table 9.
Taxonomic status of seventeen families of skates and rays according to the rankings proposed by Utinomi (1956): A = groups which have been well investigated in the whole area and almost all existing species have been already described; B = groups which have been fairly well investigated and are well known, but the investigation has not been completed; C = groups which have been partly or locally investigated, but the investigation has been incomplete, and the number of species in the group may grow larger.

Rank	Family or Genus
A	Pristidae
A	Torpedinidae
B	Narcinidae
B	Narkidae
B	Rhinobatidae
A	Platyrhinidae
A	Rhynchobatidae
A	Rhinidae
A	Pseudorajidae
A	Rajidae
C	*Dasyatis*
B	*Himantura*
A	*Hypolophus*
A	*Taeniura*
A	*Urogymnus*
B	Urolophoides
B	Gymnuridae
B	Urolophidae
B	Hexatrygonidae
B	Myliobatididae
B	Rhinopteridae
B	Mobulidae

Japan by Asahida and Ida (1988). Chen and Chung (1971) and Shen (1984) recorded *T. nobiliana* Bonaparte from Taiwan. However, it is unusual that a deep-sea electric ray has such a wide distribution from the Atlantic to the Indo-Pacific. Judging from figures of their specimens, this might be more correctly identified as *T. tokionis*. Annandale (1909) recorded *T. marmorata* Risso from Indian waters, but Monkolprasit (1984) did not include the species in her Thailand fauna of skates and rays. I believe that only one species, *T. tokionis* in this monogeneric family, is distributed in this area.

Narcinidae

Two genera and seven species have been recorded from the western North Pacific (Table 10). However, the validity of some *Narcine* species seems to be doubtful, because they are usually distinguished from one another only by the dorsal coloration of the disc.

Fowler (1941) synonymized a valid Indian species, *N. indica* Henle with *N. maculata* (Shaw) without valid argumentation, and considered that only three species, *N. lingula* Richardson, *N. maculata* (Shaw), and *N. timlei* Schneider were found in the western North Pacific. In 1966, Bessednov described *N. brevilabiata* and *N. prodorsalis* from the Tonkin Gulf, based on a single specimen of each.

According to his description, *N. prodorsalis* differs from other *Narcine* species by its first dorsal fin, which is anterior to the distal margin of the pelvics, and by the coloration of the dorsal side of its disc. *Narcine brevilabiata* differs from other Narcine species by its shorter anterior nasal lobe and by a strong concave rear margin of the pelvics. Bessednov (1966) also considered that *N. lingula*, as identified by Liu (1932), was a junior synonym of *N. brevilabiata*. Monkolprasit (1984) recorded seven species of electric rays from Thai waters and pointed out that the dorsal fin of her specimen of *N. prodorsalis* was not located anteriorly to the distal margin of pelvics. Also, she stated that, in *Temera hardwickii*, there was variation between males and females in the shape of the rear margin of the pelvics. Thus the diagnostic characters of *N. brevilabiata* and *N. prodorsalis* appear to be weak. Judging only from the figures of both species in Bessednov (1966), I believe that two different species appear in the figures. His new species, *N. brevilabiata* (fig. 8), seems to be a color variant of *N. maculata* (fig.

Table 10.

List of the species in each family of skates and rays in the western North Pacific. Numbers in parenthesis show number of species in each family.

Pristidae (4)
- *Anoxypristis cuspidatus* (Latham)
- *Pristis microdon* Latham
- *Pristis pectinatus* Latham
- *Pristis zijsron* Bleeker

Torpedinidae (2)
- *Torpedo tokionis* (Tanaka)
- *Torpedo californica* Ayres

Narcinidae (7)
- *Benthobatis moresbyi* Alcock
- *Narcine brevilabiata* Bessednov
- *Narcine brunnea* Annandale
- *Narcine lingula* Richardson
- *Narcine maculata* (Shaw)
- *Narcine prodorsalis* Bessednov
- *Narcine timlei* (Schneider)

Narkidae (4)
- *Crassinarke dormitor* Takagi
- *Narke dipterygia* (Schneider)
- *Narke japonica* (Schlegel)
- *Temera hardwickii* Gray

Rhinobatidae (6)
- *Rhinobatos formosensis* Norman
- *Rhinobatos granulatus* Cuvier
- *Rhinobatos hynnicephalus* Richardson
- *Rhinobatos microphthalmus* Teng
- *Rhinobatos schlegelii* Müller and Henle
- *Rhinobatos thouini* (Anonymous)

Platyrhinidae (2)
- *Platyrhina limboonkengi* Tang
- *Platyrhina sinensis* (Schneider)

Rhynchobatidae (1)
- *Rhynchobatis djiddensis* (Forskål)

Rhinidae (1)
- *Rhina ancylostoma* Schneider

Pseudorajidae (25)
- *Bathyraja abyssicola* (Gilbert)
- *Bathyraja aleutica* (Gilbert)
- *Bathyraja andriashevi* Dolganov
- *Bathyraja bergi* Dolganov
  - (= *B. pseudoisotrachys* Ishihara and Ishiyama)
- *Bathyraja caeluronigricans* Ishiyama and Ishihara
- *Bathyraja diplotaenia* (Ishiyama)
- *Bathyraja fedorovi* Dolganov
- *Bathyraja isotrachys* (Günther)
- *Bathyraja lindbergi* Ishiyama and Ishihara
- *Bathyraja maculata* Ishiyama and Ishihara
- *Bathyraja matsubarai* (Ishiyama)

Pseudorajidae (continued)
- *Bathyraja minispinosa* Ishiyama and Ishihara
- *Bathyraja notoroensis* Ishiyama and Ishihara
- *Bathyraja parmifera* (Bean)
- *Bathyraja simoterus (Ishiyama)*
- *Bathyraja smirnovi* (Soldatov and Pavlenko)
- *Bathyraja trachouros* (Ishiyama)
- *Bathyraja tzinovskii* Dolganov
- *Bathyraja violacea* (Suvorov)
- *Notoraja subtilispinosa* Stehmann
- *Notoraja tobitukai* (Hiyama)
- *Rhinoraja kujiensis* (Tanaka)
- *Rhinoraja longicauda* Ishiyama
- *Rhinoraja odai* Ishiyama
- *Rhinoraja taranetzi* Dolganov
  - (= *B. hubbsi* Ishihara and Ishiyama)

Rajidae (17)
- *Anacanthobatis borneensis* Chan
- *Anacanthobatis donghaiensis* (Deng, Xiong and Zhan)
- *Anacanthobatis melanosoma* (Chan)
- *Anacanthobatis nanhaiensis* (Meng and Li)
- *Anacanthobatis stenosoma* (Li and Hu)
- *Raja* (*Amblyraja*) cf. *badia* Garman
- *Raja* (*Dipturus*) *gigas* Ishiyama
- *Raja* (*Dipturus*) *kwangtungensis* Zhu
- *Raja* (*Dipturus*) *macrocauda* Ishiyama
- *Raja* (*Dipturus*) *pulchra* Liu
- *Raja* (*Dipturus*) *tengu* Jordan and Fowler
- *Raja* (*Okamejei*) *acutispina* Ishiyama
- *Raja* (*Okamejei*) *boesemani* Ishihara
- *Raja* (*Okamejei*) *hollandi* Jordan and Richardson
- *Raja* (*Okamejei*) *kenojei* Müller and Henle
- *Raja* (*Okamejei*) *meerdervoortii* Bleeker
- *Raja* (*Okamejei*) *schmidti* Ishiyama

Dasyatididae (29)
- *Dasyatis acutirostra* Nishida and Nakaya
- *Dasyatis akajei* (Müller and Henle)
- *Dasyatis bennettii* (Müller and Henle)
- *Dasyatis brevicaudatus* (Hutton)
- *Dasyatis izuensis* Nishida and Nakaya
- *Dasyatis kuhlii* (Müller and Henle)
- *Dasyatis laevigatus* Zhu
- *Dasyatis laosensis* Roberts and Karnasuta
- *Dastatis lata* (Garman)
- *Dasyatis navarrae* (Steindachner)
- *Dasyatis sinesis* (Steindachner)
- *Dasyatis ushiei* Jordan and Hubbs
- *Dasyatis violaceum* (Bonaparte)
- *Dasyatis zugei* (Müller and Henle)
- *Himantura bleekeri* (Blyth)

Dasyatididae (continued)
- *Himantura gerrardi* (Gray)
- *Himantura imbricata* (Schneider)
- *Himantura krempfi* Chabanaud
- *Himantura microphthalmus* (Chen)
- *Himantura signifer* Compagno and Roberts
- *Himantura uarnak* (Forskål)
- *Hypolophus sephen* (Forskål)
- *Taeniura lymma* (Forskål)
- *Taeniura melanospilos* (Bleeker)
- *Taeniura meyeni* Müller and Henle
- *Urogymnus asperrima* (Schneider)
- *Urolophoides giganteus* Soldatov and Lindberg
- *Urolophoides matsubarai* (Miyoshi)
- *Urolophoides multispinosus* Tokarev

Gymnuridae (4)
- *Aetoplatea zonurus* Bleeker
- *Gymnura crooki* Fowler
- *Gymnura japonica* (Temminck and Schlegel)
- *Gymnura poecilura* (Shaw)

Urolophidae (3)
- *Urolophus aurantiacus* Müller and Henle
- *Urotrygon daviesi* Wallace
- *Urotrygon marmoratus* (Zhu, Hu and Li)

Hexatrygonidae (5)
- *Hexatrgon bickelii* Heemstra and Smith
- *Hexatrygon brevirostra* Shen
- *Hexatrygon longirostrum* (Zhu and Meng)
- *Hexatrygon taiwanensis* Shen
- *Hexatrygon yangi* Shen and Liu

Myliobatididae (7)
- *Aetobatus flagellum* (Schneider)
- *Aetobatus narinari* (Euphrasen)
- *Aetobatus reticulatus* Teng
- *Aetomylaeus maculatus* (Gray)
- *Aetomylaeus nichofii* (Schneider)
- *Aetomylaeus vespertilio* (Bleeker)
- *Myliobatis tobijei* (Bleeker)

Rhinopteridae (3)
- *Rhinoptera hainanica* Zhu
- *Rhinoptera javanica* Müller and Henle
- *Rhinoptera sewelli* Misra

Mobulidae (5)
- *Manta birostris* (Walbaum)
- *Mobula eregoodootenkee* (Cuvier)
- *Mobula japanica* (Müller and Henle)
- *Mobula tarapacana* (Philippi)
- *Mobula thurstoni* (Lloyd)

1), and another new species, *N. prodorsalis* (fig. 5) is similar to *N. timlei* (fig. 3), but has larger spots. According to the original figure of *N. lingula* published by Whitehead (1970), this species also shows a close resemblance to *N. maculata*. At least, *N. lingula*, as identified by Liu (1932) seems to be identical with *N. maculata*. From examination of figures of *Narcine* species in Monkolprasit (1984), it appears that she may have identified some of her specimens incorrectly. Her specimen of *N. prodorsalis* (fig. 77) is identical with that of *N. timlei* (fig. 78), and her specimen of *N. indica* (fig. 79) is identical with that of *N. maculata* (fig. 80). It is reasonable that we should restudy the fauna of *Narcine* species of the western North Pacific, including two Indian species, *N. brunnea* and *N. indica*.

Narkidae

Two genera and four species have been described or recorded from the western North Pacific (Table 10). The classification of the four species is not questionable. However, the validity of the genus *Crassinarke*, which has not been supported by other authors, should be restudied. In this connection, the validity of the Indian genus *Bengalichthys* Annandale, which was rejected and synonymized with the genus *Narke* Kaup by Garman (1913), should also be reinvestigated.

Rhinobatidae

One genus with at least six species may be distributed in the western North Pacific (Table 10). Norman (1926) revised the world-wide species of the genus *Rhinobatos* and considered that three species, *R. formosensis*, *R. hynnicephalus*, and *R. schlegelii*, were valid in the western north Pacific. Herre (1955) recorded five additional species, *R. armatus*, *R. granulatus*, *R. halavi*, *R. obtusus*, and *R. thouini* from Philippine waters. Of these, *R. halavi* and *R. armatus* were recorded without any specimens. The specimen of *R. obtusus* in figures 5 and 6 in his paper might in fact be *Rhynchobatis djiddensis*, because of the homocercal caudal fin and the first dorsal fin just above the pelvics. Zhu (1960) recorded *R. granulatus* from Chinese waters, and Monkolprasit (1984) recorded *R. granulatus* and *R. thouini* from Thai waters. Teng (1960) described *R. microphthalmus* from Taiwan, and stated that the species was close to *R. granulatus*. The holotype of the species seems to be identical to *R. granulatus* as recorded by Zhu (1960, fig. 118). Unfortunately, the holotype of *R. microphthalmus* was lost (H. C. Yang, Kaohsiung Branch, Taiwan Fisheries Research Institute, pers. commun., 1987). *Rhinobatos granulatus*, *R. microphthalmus*, and *R. thouini* differ from *R. formosensis*, *R. hynnicephalus*, and *R. schlegelii* by possessing scapular thorns on their disc. The author tentatively considers that there are three species with scapular thorns on the disc and three species without scapular thorns in the western North Pacific. However, the relationships of the former three species with scapular thorns must be restudied. Misra (1953) reported *R. annandalei*, *R. armatus*, *R. granulatus*, *R. lionatus*, *R. obtusus*, and *R. thouini* from Indian waters and Gloerfelt-Tarp and Kailola (1984) reported some species of *Rhinobatos* from the north eastern border of the Indian Ocean. The relationships of the western North Pacific *Rhinobatos* should be restudied as well as the material from Indian waters and those from the north eastern border of the Indian Ocean.

Platyrhinidae

One genus with two species has been described and recorded from the western North Pacific (Table 10). Both species are distinguished by the number of series of tail thorns. A more detailed investigation concerning the relationships of the two species is required.

Rhynchobatidae

This monogeneric family contains only one Indo-Pacific species, *R. djiddensis* (Forskål). *Rhynchobatis yentinensis* Wang was already synonymized with *R. djiddensis* by Zhu (1960). The interrelationships between *R. djiddensis* and an Atlantic species of the genus, *R. luibberti* Ehrenbaum, should be restudied from a zoogeographical viewpoint.

Rhinidae

There is only one Indo-Pacific species of Rhinidae, *R. ancylostoma*.

Pseudorajidae

Three genera and 25 species have been described and recorded from the western North Pacific (Table 10). This family has been well studied by many authors including Ishiyama (1958, 1967) and Ishihara and Ishiyama (1985), and seems to have some problems in its systematics. Although Ishihara and Ishiyama (1985) described two species, *Bathyraja pseudoisotrachys* and *B. hubbsi*, both species had been already described as *B. bergi* and *Rhinoraja taranetzi* by Dolganov (1983) (Stehmann 1987).

Rajidae

Four genera and subgenera with 17 species have been described and recorded from the western North Pacific (Table 10). This family has been well studied by many authors including Ishiyama (1958, 1967) and Ishihara (1987). In my revised study for the western North Pacific *Raja*, I overlooked a Japanese species, *R. atriventralis* Fowler, 1934. The examination of the type of the species, USNM 75876, revealed that this species is identical with *R. kenojei* Müller and Henle (Fig. 1).

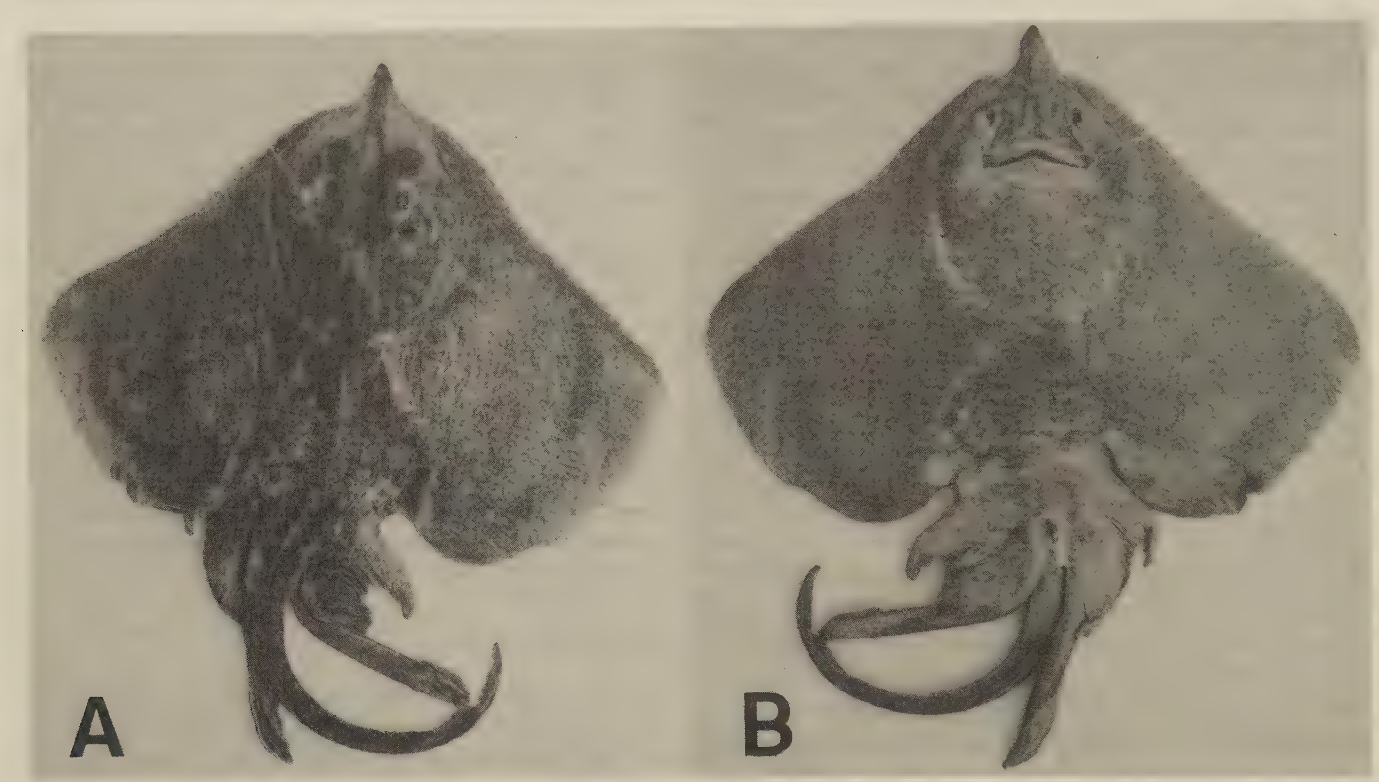

Figure 1.
The holotype of *Raja atriventralis* Fowler, 1934. USNM 75876, adult male, 412 mm TL, ? Japan, collected by P. L. Jouy. A, dorsal side; B, ventral side.

Anacanthobatis borneensis, *A. donghaiensis*, *A. melanosoma*, *A. nanhaiensis*, and *A. stenosoma* were described from the study area. Two of them, *A. borneensis* and *A. melanosoma*, might be valid (Ishihara 1984, and unpubl. data), but the other three species must be restudied in order to ascertain their validity. Gloerfelt-Tarp and Kailola (1984) reported a few as yet undescribed species of the subgenus *Okamejei* Ishiyama from the northeastern border of the Indian Ocean. Thus this area seems to be important for future studies of the systematics of the genus *Raja*. Also, species of the genus *Pavoraja* Whitley from this family might well be found in this area.

Dasyatididae

This family is discussed below by generic ranks.

Genus *Dasyatis* Rafinesque

This genus is to me the most problematical taxon in this area and in this family. At least 14 out of 33 species (after Fowler 1969b, 1970; Compagno and Roberts 1984) are distributed in the western North Pacific (Table 10). *Trygon carnea* Richardson was already synonymized with *D. bennettii* (Müller and Henle) by Fowler (1941) and *D. atratus* Ishiyama and Okada with *D. violaceum* (Bonaparte) by Wilson and Beckett (1970). *Dasyatis cheni* Teng was synonymized with *D. zugei* (Müller and Henle) by Nishida and Nakaya (1988). Species of Indo-Pacific *Dasyatis* are usually widely distributed. Information on their specific characters and morphological variation has been meager. Any revisional study concerning the species of this genus should be conducted using material from the entire Indo-Pacific region.

Genus *Himantura* Müller and Henle

At least seven species of this problematical taxon may be distributed in this area out of 17 species in the world (after Compagno and Roberts 1982) (Table 10). Among these, *H. microphthalmus* Chen seems to belong to the genus *Dasyatis* rather than *Himantura*, and might be a senior synonym of *Dasyatis acutirostra* Nishida and Nakaya. These species need to be restudied on the basis of material from the entire Indo-Pacific region. For instance, Annandale (1909) described *Trygon alcocki*, *T. jenkinsi*, and *T. fava* (as *favus*) from the Indian waters. However, it is likely that *T. fava* might be a color variant of *Himantura uarnak* (Forskål), judging from the figure of the type of the species (See Annandale 1909, fig. 3 in pl. 1).

Genus *Hypolophus* Müller and Henle

This monotypic genus has one Indo-Pacific species, *H. sephen*.

Genus *Taeniura* Müller and Henle

Three species have been described and recorded from the western North Pacific (Table 10). All three species are clearly distinctive from one another. *Taeniura brockii* Schultz and *T. maculata* Miyoshi were already synonymized with *T. melanospilos* Bleeker by Teng (1962).

Genus *Urogymnus* Müller and Henle

This monotypic genus has one Indo-Pacific species, *U. asperrimus*.

Genus *Urolophoides* Lindberg

This genus is endemic to the northern part of the western North Pacific with three species (Table 10). However, the relationships of three species have not been studied and the validity of the genus itself was considered doubtful (Bigelow and Schroeder 1953). Thus the interspecific comparison of the species and the relationships of the genus to the other genera should be restudied.

Gymnuridae

Two genera with four species have been described and recorded from the western North Pacific (Table 10). Both genera are distinguished by the presence or absence of a dorsal fin. *Pteroplatea jordani* Zhu was synonymized with *Gymnura bimaculata* (Norman) by Zhu (1960) and later *Gymnura bimaculata* (Norman) was synonymized with *G. japonica* (Temminck and Schlegel) by Isouchi (1977). *Gymnura crooki* was described by Fowler (1934). The holotype of the species, USNM 6830, however, should be reexamined as the species seems to be a junior synonym of *G. japonica*. *Gymnura micrura* Schneider was recorded by Monkolprasit (1984) from Thai waters. It is questionable whether this Atlantic species also occurs in Thailand waters. The record of *G. micrura* from Indian waters by Day (1878, 1889) and Misra (1953) may be doubtful for the same reason.

Urolophidae

Two genera with three species have been described and recorded from the western North Pacific (Table 10). *Urotrygon daviesi*, which was originally described from South Africa by Wallace (1967), has been recorded from Hawaii (Tinker 1978) and from Japanese waters (Nakaya 1982). Zhu and Meng (1981) described *Urolophus* (= *Urotrygon*) *marmoratus* from Chinese waters. However, the validity of the species may be doubtful, because the species is quite similar in shape to *U. daviesi*, which has an Indo-Pacific distribution. *Urotrygon mundus* Gill was recorded from Taiwan waters by Chen and Chung (1971) and Shen (1984), although the species is distributed in the eastern Pacific. Judging from the figure of the specimen, Chen and Chung (1971) might have misidentified their specimen of *U. daviesi* as *U. mundus*. The specimen identified as *U. mundus* by Shen (1984) might be a species of the genus *Urolophus* of uncertain identity.

Hexatrygonidae

This monogeneric family consists of five species at present and all five species have been described and recorded from the western North Pacific (Table 10). In 1980, Heemstra and Smith described a sixgill stingray, *H. bickelli*, from South Africa and a year later Zhu and Meng (1981) described another species of the genus from Chinese waters. Since then three species of *Hexatrygon* have been described from the area (Shen and Liu 1984; Shen 1986a, b). It is not natural that so many species of a monogeneric family occur sympatrically in such a small area. Recently, even *H. bickelli* was recorded from the South China Sea (Zhu and Meng 1982). A review of the relationships of these five species is needed.

Myliobatididae

Three genera and seven species have been described and recorded from the western North Pacific (Table 10). The genus *Aetobatus* Blainville has a single series of teeth and a caudal spine, the genus *Aetomylaeus* Garman has seven series of teeth and no caudal spine, and the genus *Myliobatis* Cuvier has seven series of teeth and a caudal spine.

Aetobatus reticulatus was described by Teng (1962), stating that the species had a single series of teeth and no caudal spine. He even suggested that a new genus should be established for the species. Judging from his figure of the type specimen, however, the species shows a close resemblance to *Aetomylaeus vespertilio* Bleeker, though both species currently belong to a different genus. Moreover, there is a strong possibility that *A. vespertilio* Bleeker is a junior synonym of *A. maculatus* (Gray and Hardwicke). *Myliobatis rhombus* was described from oriental waters by Basilewsky (1855). However, in view of the present status of the species, it is probably invalid. *Aetobatus milvus* (Müller and Henle) was recorded from Chinese waters by Zhu (1960) and Chen and Chung (1971) and from Thai waters by Monkolprasit (1984). However, the description of the species by Chen and Chung (1971) was brief, without a figure, and that provided by Zhu (1960) had no diagnostic characters and an indistinct figure. The specimen identified as *A. milvus* by Monkolprasit (1984) may have been a young *A. maculatus* (Gray and Hardwicke) since the figure of the specimen showed that white spots were present on the posterior region of its disc. Also, *Myliobatis oculeus* Richardson might be a junior synonym of *A. maculatus* (cf. Fowler 1941; Whitehead 1970, pl. II, fig. C). *Aetobatus guttatus* (Shaw) was recorded from Chinese waters by Zhu (1960). His specimen, however, seems to be misidentified as *A. narinari*, according to figure 10 in Annandale (1909), which showed a marked difference between the snout region of both species. Fowler (1941) synonymized *A. flagellum* with *A. narinari*, but the same figure in Annandale (1909) clearly showed that both species were valid.

Rhinopteridae

Three species have been recorded from the western North Pacific (Table 10). However, *R. hainanica* Zhu and *R. sewelli* Misra might be conspecific with *R. javanica* Müller and Henle. A more detailed study must be made of these three species.

Mobulidae

Two genera with five species have been described and recorded from the western North Pacific (Table 10). Notarbartolo-di-Sciara (1987) reviewed the genus *Mobula*, based on the material from all around the world, and pointed out that many systematic problems exist in this genus. According to his results, *Mobula diabolus* recorded from the western Pacific by many authors is in fact *M. eregoodootenkee* (Cuvier), *M. formosana* Teng is synonymous with *M. tarapacana* (Philippi), and *M. diabolus* as recorded by Masuda et al. (1984) seems to be in fact *M. thurstoni* (Lloyd). However, he did not establish a new genus for the species of Mobulids which lack a caudal spine.

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Workshop on Fisheries Management

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Introduction

The Workshop on Fisheries Management was moderated by Emory D. Anderson and Kazuyuki Teshima. The following is a distillation of the open discussion that took place on 13 December 1987 involving all participants.

Worldwide catches of elasmobranchs are increasing, as described in several of the papers presented. However, decreases in Japanese landings of elasmobranchs in recent years (190,000 t in 1947 to 35,000 t in 1986) are of concern and may have resulted from overexploitation. There are numerous documented cases of elasmobranch fisheries (primarily for various shark species) in different parts of the world that have come and gone rather quickly, demonstrating the inability of these species to support intensive fisheries on a sustainable basis. There is a clear need, at least from the biological point of view, to manage elasmobranch fisheries. Unfortunately, there has been very little, if any, management of fisheries involving these species, and future prospects are uncertain. However, one of the aims of this conference was to emphasize this need and to suggest possible approaches to managers.

Data Needs

Biological and fishery data are essential for the assessment and management of any exploited marine species. Some of the papers presented reported on the significant progress made in the investigation of age and growth of elasmobranchs in the last 5–10 years. This progress is commendable, but such information alone is insufficient to satisfy the data requirements for assessment and management, as identified in several papers presented. The need for adequate biological data and fishery statistics cannot be overemphasized. Strong commitments at national levels coupled with international cooperation will be necessary to acquire this information if the management of elasmobranch resources on a broad scale is to be achieved.

Data needs that have been identified include the following:

- stock identification,
- age and growth,
- catch statistics (commercial and recreational),
- catch per unit effort (CPUE) or fishing effort,
- fishery sampling data (length, weight, sex, age, and maturity),
- natural mortality estimates,
- recruitment estimates,
- reproductive capability,
- fishery-independent estimates of stock size and recruitment,
- mark-and-recapture results,
- social and economic aspects of the fisheries.

Assessment Approaches

Many of the classical models developed to assess finfish stocks may not be appropriate for use on elasmobranch stocks because biological processes such as growth and reproduction considered implicitly in those models differ considerably between the two groups of fish. Models used to assess cetaceans may be more applicable, although it was questioned whether such models were sufficiently developed for use on elasmobranch data and whether data collection programs for elasmobranchs should be modified to ensure the proper use of such models.

Analytical models have been used extensively to assess cetacean stocks and provide a basis for management by the International Whaling Commission. Many of these were fishery models modified for use on cetaceans. Through gradual modifications, some of these have evolved to resemble models employed for terrestrial mammal populations. There is an abundance of data on which to base analytical assessments for many of the major cetacean stocks, but in other cases, even with the use of sophisticated models, the assessment results are uncertain because of insufficient or questionable data. This limitation applies to finfish stocks as well. In the absence of appropriate data, the very best model is no better than a dartboard.

Some of the analytical models developed for use on finfish stocks can also be used on elasmobranch stocks if the appropriate input data are available. For example, the Schaefer stock-production model, one of the simplest models for teleosts, which requires only a time series of catch and effort (or CPUE) data, may be applicable for use on an elasmobranch stock providing that a sufficiently long (e.g., 20–30 years) time series of data is available. Unfortunately, such a time series for an individual elasmobranch stock is not known to exist. However, one of the shortcomings of a stock-production model is that it provides only a limited amount of useful information (e.g., an estimate of maximum sustainable yield (MSY) under equilibrium conditions, which rarely, if ever, exist). Otto et al. (1977) and Anderson (1980) attempted to estimate the MSY of large sharks in the Western North Atlantic using the combined international catch (reported and estimated unreported) of a mixture of species/stocks and effort data from the Japanese longline fishery, but the results are totally uncertain owing to the use of questionable data and the unknown impact of fishing effort on multiple species/stocks.

Stock-production models are more practical and useful in the early stages of assessment when a data base is developing. Later, when more extensive data bases are available (e.g., age composition of the catch), assessments should be done with more analytical or age-structured models such as virtual population analysis (Gulland 1965) or cohort analysis (Pope 1972). Such models provide past and present estimates of age-specific fishing mortality rates and stock sizes and permit the forecasting of future catches and stock sizes. This type of approach is presently used on numerous finfish stocks in the Northeast Atlantic that are assessed by the International Council for the Exploration of the Sea (ICES) (Anonymous 1988) and managed on the basis of total allowable catches (TAC) established annually.

Analytical assessments of this type are possible for elasmobranchs given the proper data, but the accumulation of such data would require extensive commercial and recreational catch sampling programs and laboratory analysis (e.g., ageing). In the absence of such data bases at the present time, concern was expressed as to how the size of elasmobranch stocks could be estimated. Anderson (1990), in discussing fishery models applied to elasmobranchs, suggested fishery-independent surveys (trawls, longlines, etc.) and mark-and-recapture experiments as means to obtain stock size estimates. The wide-ranging distribution of many species of sharks would also require knowledge of stock identification. It was also suggested that the direct stock-recruitment relationship in sharks might prove to be useful in obtaining abundance estimates for some species in a way not possible with teleosts. The presence of nursery areas for some shark species that have limited distributional ranges, in which the young remain localized for a sufficient period, would permit tag/recapture studies for estimating first the abundance of the young and second (knowing litter sizes and sex ratios) the abundance of the parent stock. Such an approach would not be feasible in the case of a wide-ranging species.

The Far Seas Fisheries Research Laboratory, Fisheries Agency of Japan, conducts basic research and assesses the status of the demersal finfish stocks in the North Pacific. Single-species models are used primarily to assess these stocks. However, work has recently begun on the development of ecosystem models to investigate the interrelationships among the demersal stocks, marine mammals, and birds in the Bering Sea. The possibility of applying such a model to investigate the relationships between sharks and their prey was suggested. Since the Laboratory is also involved in investigations on the population dynamics of marine mammals, it was suggested that attempts should be made to encourage the application of this expertise to some of the elasmobranch stocks. This possibility was acknowledged, but would require additional funding. It was also pointed out that the Laboratory places considerable emphasis on tuna research and assessment, but little or none on elasmobranch research because of the low value of the resource.

Bycatch and Discards

The catch of sharks is about one-third of the tuna/billfish catch in the Japanese longline fisheries. Longlines fished near the surface take spearfish, billfish, and pelagic sharks; whereas longlines fished in deeper waters for tuna take deep-water shark species. The majority of Japanese longline effort has been directed towards tuna in the Pacific and, consequently, has taken primarily deep-water sharks. The Japanese shark catch in the Pacific has, therefore, been only about 30% of the relatively high level in the Atlantic, where more longline effort has been directed towards billfish and has resulted in higher catches of sharks which are more prevalent near the surface.

Records indicate that the bycatch of sharks in the Japanese pole and line fishery for skipjack tuna is very low or nonexistent, although sharks cause considerable damage to the hooked tuna.

Specific information on the general distribution of individual species of sharks taken as bycatch in longline fisheries is difficult to obtain, although some data for certain species based on Japanese records do exist from the Pacific. In the Atlantic, the various longline fisheries (e.g., Japanese tuna and U.S. swordfish) generally operate in specific areas, and the shark bycatch depends on the area and the target species. U.S. swordfishermen experience a higher shark bycatch than do Japanese tuna longliners. Even though the percentage of shark bycatch in the Japanese longline fishery in the Atlantic is relatively low, the numbers taken are excessive in the view of U.S. recreational fishermen.

Many of the elasmobranchs taken as bycatch in fisheries directed towards other species are discarded. Estimates of the extent of the discarded shark bycatch in some fisheries (e.g., longline fisheries for billfish/tuna and U.S. recreational fishery) were reported in some of the papers presented. Records from the training vessels of Japanese fisheries and from many commercial vessels suggest that about 25% of the shark catch in their longline fisheries is landed and reported and the rest is discarded. Additional sources of shark bycatch and discard were identified (e.g., hake fishery off South Africa), with indications that quantitative estimates were potentially available.

The survivability of discarded sharks, particularly in the longline and recreational fisheries, was discussed. Survival of released sharks depends on many factors, such as species, time on the hook, depth of water, etc., but based on data obtained from Japanese longline vessels operating within the U.S. Fishery Conservation Zone (FCZ) in the Atlantic, it is relatively high (e.g., survival on the line may be 70% or higher for blue sharks). More reliable data on survival may be available in the future from experimental longline surveys conducted for tag/release studies. Recent survey results indicate that 55–75% of the sharks caught in the U.S. recreational fishery are discarded alive (Hoff and Musick 1990). Although a high proportion of many shark species caught either by longline or recreational fishing (e.g., rod and reel) have been observed to be alive and in apparent good condition at the time of discarding, studies have shown that mortality often occurs later because of the effects of physiological stress. Elasmobranchs taken as bycatch in a trawl, however, are generally in very poor condition when brought aboard the fishing vessel and the survival rate of discards is extremely low. Data indicate differences among species in survivability. It was suggested that the available survival potentials of different shark species following hook release should be compiled.

Research Funding

Research on elasmobranchs has generally been assigned relatively low priority by most countries and funding organizations. Much of the work done to date has been possible only because of the efforts of innovative investigators and/or fortuitous circumstances which have allowed studies to be funded from sources designated primarily for other purposes. Elasmobranch research is not receiving the priority consideration that it requires. Even though the market value of elasmobranchs as a whole is far less than that of finfish, evidence is rapidly accumulating on the delicate nature of these animals, in terms of their susceptibility to overexploitation and rapid depletion, on their importance in marine ecosystems, and on their value as food sources and bio-medical research subjects. Increased funding and higher priority for elasmobranch research are, consequently, necessary and should be recommended. Data collection at the species level from both commercial and recreational fisheries must be improved. Further biological and life-history information and knowledge on stock status and responses to fishing are desperately required, as is the proper implementation of this knowledge towards the effective management of the resources.

Management Issues

Questions were raised as to the minimal amount of information required to assess and/or manage an elasmobranch stock. Even though U.S. law requires using the best available data in developing fishery management plans, the data available on most elasmobranchs are grossly inadequate from the biological point of view. Must major data collection programs be implemented before assessment and management are possible? Managers must ultimately decide whether there is a need to manage a given stock or fishery and whether the scientific knowledge is sufficient to provide a proper basis for any envisaged regulations.

The assessment and management of sharks or other elasmobranchs must require some knowledge of their stock identification. As little is known about this, it was recommended that (1) tagging studies should be conducted to provide better information on distribution, migration patterns, stock structure, and growth and that (2) population genetics should be investigated further as a tool for stock separation making use of some of the new and powerful electrophoretic and mitochondrial DNA techniques. International cooperation and collaboration in both of these areas of study are necessary because of the wide-ranging nature of shark species.

The social and economic value of recreational fisheries for sharks was emphasized. On the east coast of the United States, the growing recreational fishery for sharks is currently much more important economically than the commercial fishery. Summer shark tournaments have been and will continue to be excellent sources for catch-rate data and various types of biological information. The potential political power and influence of the recreational fishing industry, if motivated, organized, and effectively focused, with a thorough economic evaluation of the recreational shark fishery, could be very instrumental in encouraging the serious consideration of an active conservation and management program for sharks by the U.S. Federal Government. In some areas and for some species, the growing importance of recreational fishing for sharks may lead to the sharp reduction or elimination of commercial fishing for sharks in future management plans.

There is generally a stronger motivation for the implementation of a management plan when the resource in question is depleted than when it is abundant. From the management point of view, the use of analytical models that would only provide estimates of MSY (even if encompassing geographical areas which may include multiple stocks of a given species) would be acceptable, because even that would represent a major step forward from the present state of knowledge. The estimation of MSYs would probably lead to management based on catch quotas which, for some areas, would be allocated to user groups such as domestic commercial fishermen, domestic recreational fishermen, or foreign commercial fishermen. It was questioned whether sharks would be better managed by means of catch quotas or minimum size limits. The latter approach was considered impractical given the wide range in sizes of adult sharks (i.e., the young of some species are the same size as the adults of other species and multiple species are taken by most fisheries).

The lack of elasmobranch management and the low priority given to research and data collection in their fisheries has been attributed to their low value relative to most finfish or to the perception that their abundance is not low and hence does not require any remedial action. However, in the case of sharks, once it has been determined that stock abundance is low, it is probably too late for the stock to benefit from management. The low market value of sharks is a weak guideline on which to base a decision to manage or not manage them, given the fact that they are obviously a key element in the marine ecosystem. Managers must consider what effect the annual removal from the world's oceans of over 1/2 billion apex predators that cannot be replaced for 20–30 years has on the remaining animals. There are numerous examples of the adverse effects that have followed the creation of ecological imbalances. Along the South African coast of Natal, the annual beach netting and removal of over 2,000 large sharks at a yearly cost of over $2 million has resulted in a population explosion of an undesirable smaller species of shark. In terrestrial ecosystems, there are documented population explosions of prey animals (e.g., Kaibab deer in Arizona) with undesirable aftermaths (starvation and population decline) following the drastic reduction of their predators (e.g., wolves, coyotes, cougars). Based on these and other unfortunate experiences and our current knowledge of the fragility of elasmobranch stocks, it is irresponsible not to manage them properly, simply because they are perceived to be economically unimportant.

Attitudes and Uses

Public attitude towards elasmobranchs (particularly sharks) is a major reason for their low priority. For example, in Guam, the Mariana Islands, and Christmas Island, as well as many other areas, it is perceived that the only good shark is a dead shark, and sharks are not considered to be recreational species. This attitude contrasts with that in other Pacific cultures where sharks are appreciated or at least tolerated. Sharks are feared because of damage done to fishing gear and and because of attacks to humans on swimming beaches. According to Polynesian legend, the mako shark is the reincarnation of a human; consequently, it is treated with respect as a god or as a family member. Sharks are not sought after as a food product or by-product in Hawaii, but are perceived to be dangerous because of encounters with them on public beaches which have resulted in bounties and eradication programs. In many other parts of the world, sharks are similarly feared and thus hated. Fishermen for other species view them as competitors. Such attitudes must change before funding priorities will improve.

Attitudes towards sharks, the perceptions of their economic, ecological, and cultural value, and the concerns for increased support and funding for research, data collection, and management expressed at this meeting, reflect primarily the views of only two major countries, Japan and the United States. These two countries, among the most rich and powerful in the world, account for only about 10% of the world's catch of cartilaginous fishes. Fisheries involving elasmobranchs are conducted in many different ways, under different conditions, and for different reasons in other countries. The diverse attitudes, fisheries, and uses of sharks throughout the world need to be kept in proper perspective when considering future management and controls on fisheries. As mentioned previously, however, proper management of elasmobranchs must be done on a stock or population basis, taking into account their wide distributions which frequently traverse national boundaries.

Consideration was given to some of the important uses of elasmobranchs. They represent an important food source as well as a source of various by-products used for cosmetics, and biomedical applications. Biomedical applications may be most important in cancer research. The similarity and uniqueness of the various biological systems in elasmobranchs make them very useful in general studies with human application. These would include, for example, studies on cartilage, neuroreception, olfaction, ionic regulation, and hormone receptors.

The possibility of developing specialized fisheries for some of the deep-sea shark species was suggested as a source for highly edible flesh and by-products such as squalene. In some cases, the estimated biomass levels would appear sufficiently high to support fisheries. However, it was felt that fisheries on these deep-sea shark resources should not be encouraged as they would very likely succumb to fishing pressure in a relatively short time, as have most other shark stocks similarly exploited. Furthermore, the development of fisheries on sharks to provide a specific by-product such as squalene is not justified because it can generally be synthesized relatively inexpensively.

Summary

The Workshop stimulated useful discussion on data requirements and analytical approaches for assessment and management, provided a forum for the further elaboration of topics and questions raised in various papers presented during the conference, and produced suggestions of broad topics for further research and collaborative investigation by U.S. and Japanese participants. It is hoped that this and other reports and papers presented at or resulting from this U.S.–Japan Workshop on Elasmobranchs as Living Resources will have a positive impact and influence on decision-makers in these and other countries and will lead to an enhanced attitude concerning the need to support further research and data collection on elasmobranchs and to more seriously consider the need for initiating management programs for these important resources.

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Age and Growth, Reproduction, Shark Tagging, and Systematics

As Tom Hoff, Emory Anderson, and others have pointed out in this volume, accurate information is needed on each elasmobranch stock to understand and predict its relationship to a fishery. On a broader scale, information is needed on all elasmobranchs to understand their role in the ecology of the oceans. In our workshop sessions, much interest was given to recommendations for future research. Working groups were formed and charged with the task of producing a statement of future research needs with recommendations. The following sections are their report.

Recommendations for Research Needed to Better Understand the Age and Growth of Elasmobranchs

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It has only been in the past several decades that scientists have directly approached the question of growth rates, longevity, and age composition of elasmobranch populations. Most of this research has been stimulated by increasing interest in elasmobranchs as fishery resources. Despite the recent increase in the number of studies on elasmobranch age and growth, there are many areas of research which need prompt and serious attention.

Verification of Growth Zones in Calcified Structures

The major problem originally facing biologists studying age and growth of elasmobranch fishes was the unavailability of hard structures, such as scales or otoliths, which clearly demonstrated growth zones. Examination and use of elasmobranch vertebral centra for such purposes have produced the majority of results in this field. In other groups, such as sturgeons and bony fishes, comparisons of growth zones among different structures from the same specimens provide verification of age information. For those species with several calcified structures, such as the squaloid sharks which have vertebrae and fin spines, these cross comparisons will be important for verifying growth information.

Precision and Accuracy

Several mathematical expressions have been created to evaluate the precision of age estimates. These include the average percent error (A.P.E.) and the index of precision (D); both have been used in studies of bony fish growth, but seldom have been applied to elasmobranch studies. If the age of a specimen is known, through tag-recapture studies or laboratory rearing, accuracy can be assessed. Both precision and accuracy need to be estimated in future studies of elasmobranch age and growth.

Growth Models

A need for growth models that fit the observed length at age information is common to all fish growth studies. The von Bertalanffy growth equation is currently the most commonly used model to describe the growth of elasmobranch and other fishes. Unfortunately it fits many of the slower growing species very poorly. Some of these poor fits can be attributed to individual variation and sample size problems. Other discrepancies are due to poor fitting techniques, such as reliance on linear parameter estimation, rather than curvilinear fits, such as those obtained using Marquardt's algorithm. Some elasmobranchs exhibit the slow growth and long lives typical of cetaceans and terrestrial mammals. Growth algorithms need to be borrowed from nonteleost sources to better fit the elasmobranchs fishes.

Sample Sizes

Even though researchers have consistently attempted to obtain sufficient numbers of representative sizes of each species of elasmobranch studied, most studies have suffered from sample size and range problems. This results in inaccurate estimates of the growth model parameters. The asymptotic length (L_∞), growth coefficient (K), and the estimated age at which size is zero (t_0), all parameters of the von Bertalanffy growth equation, will be poorly estimated from inadequate samples of large and/or small individuals of a particular population. Sample size inadequacy will also detrimentally affect age composition data, which are useful for evaluating year-to-year variation in a population, especially as this is related to fishing pressure.

Individual Variation

It is well known that individuals of many vertebrate populations vary considerably in the size at which they reach a certain age, or in the age they reach by a given size. Despite this knowledge, many studies of fish growth have attempted to describe the growth rate of all individuals of a population or species with a single curve or line, ignoring individual variation. Tagging studies have demonstrated negative to extremely positive individual growth within a specific amount of time. Individual variation in elasmobranch growth patterns should be incorporated into our results.

Tagging Studies

One of the most successful age validation methods is tag and recapture analysis. This enables one to measure the specimen, remeasure it once it is recaptured, and thus calculate growth over a known time period. Additionally, marking the calcified structures of the organism with oxytetracycline (OTC) allows an evaluation of growth zone deposition periodicity. Although this approach has been successfully used with many fishes, its use with elasmobranchs has been minimal. Thus, it is a very promising method to apply in validating growth zones in calcified structures of elasmobranchs that and can be utilized in both laboratory and field studies.

New Methods of Age Determination and Verification

Despite the general use of vertebral centra and fin spines as age determination structures in elasmobranchs, additional approaches to assessing age and growth in these fishes are needed. Many species have poorly calcified skeletal structures and are difficult or impossible to age. In others, the growth zones do not appear to accurately reflect somatic growth information. Several new techniques have been developed that may be able to help fill the gap in our knowledge of the age and growth of these fishes.

Image Analysis and Computer-aided Ageing

With the advent and availability of personal computers, microscopy has been coupled with computer and video monitor technology to aid researchers in analyzing growth information from calcified structures. These systems generally use image analysis to increase objectivity and speed in estimating growth. This assumes, of course, that objective criteria for growth zones can be established at the start of the project to insure interinvestigator consistency. Also, this approach requires calibration and standardization procedures for each species and structure studied.

Electron Microprobe and Elemental Microanalysis

The technology to analyze concentrations of elements in calcified structures recently has been developed and is an additional method of verification of growth zone periodicity. This technique can be used to assess chemical differences that may be correlated with visually identified growth zones in the calcified structure. While this approach has been applied to bony fishes, it has rarely been used to evaluate elasmobranch fishes.

Radiometric Dating

Radioisotopes of some elements occur in the calcified structures of certain organisms. The decay rates of these isotopes, which are incorporated into the calcified structures over the life of the fish, can provide an independent assessment of age. This method was not entirely successful in initial studies of elasmobranch fishes, primarily because uptake of the isotopes was not constant with time. and isotope concentrations were not static after incorporation into these structures. However, it is possible that these problems may not exist for other structures or other species. Thus, this approach is worth further evaluation.

Stable Isotopes

To assess the growth history of individual organisms and the potential influence of environmental factors on growth, stable isotopes have been analyzed in calcified structures of shellfish and bony fishes. This approach has not been used for elasmobranchs, but certainly has promise. However, the same problems as discussed above for radiometric dating may apply to this method.

Tissue Protein Concentrations

Certain proteins are hypothesized to accumulate in the tissues of organisms. One of these, lipofuscin, has been proposed as an independent index of age because it appears to accumulate at a predictable rate and is not reabsorbed over the life of an organism. While experiencing methodological difficulties in its initial use as an age-determination technique, this approach has distinct promise for ageing large, fast-moving, and relatively rare organisms, such as elasmobranchs and billfishes.

Calcification Physiology

All but one of the elasmobranch species studied thus far exhibit annual growth zones in their vertebral centra and fin spines. It is extremely important to determine the physiological mechanisms responsible for this temporal deposition pattern. In a very few studies of calcification in fishes, the hormone calcitonin has been implicated as an important factor in controlling blood levels of calcium. The suggestion is that temporal periodicity of calcium uptake from food, deposition, and/or resorption among the circulatory system and tissues of vertebrates is regulated by the endocrine system via the production of hormones like calcitonin. This control most likely is moderated by at least three abiotic factors, including day length, temperature, and water chemistry, and four biotic factors, including food, predators, parasites, and competition, all of which may be density-dependent or independent. This hypothesis has been only generally approached in bony fishes and has not been tested in elasmobranchs. Thus, this research could be productive in characterizing the age, growth, and longevity of elasmobranch fishes.

Recommendations for Work Needed to Increase Our Knowledge of Reproduction Relative to Fishery Management

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Reproductive strategies are a limiting factor in elasmobranch fisheries. (See Pratt and Casey 1990.) Understanding elasmobranch reproduction is vital to the success of fisheries management. The following recommendations may serve as initial guidelines to the continuing elucidation of elasmobranch reproduction.

Size and Age at 50% Maturity

Because of differences in life histories and reproductive strategies, elasmobranch species vary greatly in their relative size and condition at reproductive maturity. The female blue shark, *Prionace glauca*, for example, first matures those organs needed for spermatozoa storage, them some months later the eggs become ripe. As a consequence of these unique strategies; the length and age that 50% of the population reaches maturity must be determined for each sex of each species. To generalize these parameters would lead to gross inaccuracies. Age should be determined by a validated methodology. Sexual maturity should be determined by the most accurate method possible. Presence of fully developed sex products is the most precise indicator. The condition of claspers and uteri are not as definitive as the presence of sperm packets in the terminal storage areas of the ductus epididymides (ductus deferens) or the presence of embryos or ovarian eggs determined to be full-term or ripe by seasonal sampling. The determination of maturity must take into account the possible seasonality of sex product development. Are the mature members of a species fertile or fecund year round or only during a mating season?

Courtship

In the future, these areas may need to be protected from fishing pressure. If sperm storage is employed by the female (as in the blue shark), it may mean that more males are available to the fishery without loss of breeding stock. The males of some species, such as the sandbar, *Carcharhinus plumbeus*, and the blue shark inflict deep wounds on the female during courtship. This possible source of mortality should be understood for inclusion in estimates of total population mortality.

Pregnancy

Reproductive mode, gestation or hatching time, and frequency of pregnancy are poorly known and have great management significance. We need to determine if gestation and embryo production are determined by temperature, a solar or lunar year, other environmental cycles, or are random. The natural sex ratio, number of embryos or eggs released, and overall fecundity must be determined. In some species the number of young increases as maternal size increases; in others, the size of young increases. In the face of a fishery, production would probably favor an increase in the numbers of young rather than the size of young if the females are allowed to attain sizes of maximum production.

Fate of the Young

The size at birth, determined by the observed size of the largest embryos and the smallest free-swimming individuals and the location at which these fish are caught, can establish the pupping area, time, and location of birth. The distribution and early migrations of neonates is of critical importance to their survival success.

Habitat Requirements

The courtship and pupping areas, whether estuary or open sea, must be defined oceanographically. The presence and abundance of prey, competition with other species, predators of young, basic water chemistry, possible pollutants and competition with man for food and space must be quantitatively described for each species of elasmobranch of sport or commercial interest.

Effects of Fishing

Does fecundity increase as stock size decreases? The size, age, and reproductive profile of the impacted population should be determined and related to how these factors affect a specific fishery. For example, does the fishery depend on immature sharks or pregnant females?

Recommendations for Future Shark Tagging Programs

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Fish tagging began about 100 years ago and by 1910 fewer than 100,000 fish of all species had been tagged. An accurate number of fish tagged since then is unknown, but it is many millions considering over 30,000,000 Pacific salmon have been released annually in recent years. In contrast, less than 400,000 sharks, including dogfish, have been tagged throughout the world during the past century and most of these have been tagged during the past three decades. Some obvious reasons for fewer tagging studies on sharks are that sharks, particularly large individuals, are difficult and expensive to capture and handle; some species range over broad geographic areas and are available for only brief, seasonal periods. In many parts of the world sharks have not been of value in traditional commercial fisheries. In addition, deep-water forms require specialized capture equipment that has been developed only recently. Moreover, it is only in the past 30 years that tagging methods have been developed that have been used successfully on sharks.

As a consequence of these obstacles, knowledge of migrations and other elements of shark biology are incomplete for nearly all species. This is generally the case despite some successful past and present tagging programs in different parts of the world, including Australia, Japan, South Africa, the U.S.A., and several European countries.

For the sake of convenience in discussing recommendations, we arbitrarily assigned shark tagging studies to the following two closely related categories: 1) *Basic Studies* which are directed toward understanding the biology and life history of a species, and 2) *Applied Studies* which are directed toward the practical application of tagging-recapture data with respect to problems of fisheries management or to evaluating the impact of human activities on sharks. In the broad sense, the eventual "applications" may vary from stringent conservation efforts to protect a species from overfishing, to reducing shark populations where they compete with or represent a danger to man.

Basic Studies

Social organization in sharks is complex and poorly understood. It is known that many species use different areas for mating, pupping, nursery grounds for juveniles, and that adults segregate by sex and often occupy entirely different areas for most of the year. Highly pelagic species are distributed over entire ocean basins. Some coastal species migrate over a wide latitudinal range, while littoral sharks may show very little movement, and deep-water species may segregate solely by depth. Tagging studies on the blue shark, *Prionace glauca*, in the North Atlantic Ocean during the past 25 years provide evidence that important mating grounds are located off North America, while the primary pupping grounds and nursery grounds for very young blue sharks are thousands of miles away off Southern Europe and Africa. Tag and recapture data from the sandbar shark, *Carcharhinus plumbeus*, an example of a coastal species, has shown north-south movements of 2,000 miles along the North American coast between the northeastern United States and Mexico. Species of littoral sharks including the nurse shark, *Ginglymostoma cirratum*, may complete their life cycles within a geographic range of less than 100 miles. Almost nothing is known about the movements and ecology of most of the bathypelagic sharks. What little is known about deep-water forms such as the cat sharks (Scyliorhinidae) suggests that they do not migrate far but segregate into different depth zones by size and sex.

Tagging programs as a means for advancing knowledge of the basic biology and ecology of sharks should include the following studies:

1. **Migrations** of important species with emphasis on delineating their migratory pathways in space and time for each segment of the population.
2. **Age and Growth** of important species to validate age estimates from anatomical parts, size-frequency data, and other ageing methods.
3. **Natural Mortality** to identify natural cycles of abundance before stocks are impacted by fisheries and to evaluate mortality from intra- and inter-species relationships that may act as natural population controls.
4. **Behavior** (including acoustic tagging) to determine diurnal and local movements, mating, and reproductive behavior, and predator-prey interactions.
5. **Habitats** (including satellite tracking and imagery) to identify and classify habitats for different life stages, particularly those habitats that are likely to be impacted by pollution, coastal development, and other human activities.

Applied Studies

The tagging of fish for studying population dynamics is credited to C. G. Peterson in 1896. Since that time, tagging as a means for estimating mortality and population size has been used as a standard tool that has been applied to a myriad of fish stocks throughout the world. Although the field of population dynamics has produced a variety of powerful analytical methods that use tagging data, relatively few tagging programs have been directed to studies of the population dynamics of large sharks.

Currently, there is growing concern for overfishing stocks of sharks in some parts of the world, while in others efforts are being made to reduce shark abundance. The effects of management incentives directed to maximizing yields or otherwise controlling shark populations are difficult to predict because in most cases fisheries data are incomplete or lacking. Tagging studies can help to fill the need for population dynamics data which are, in the case of rapidly expanding shark fisheries, particularly acute.

Future shark tagging programs should include studies designed to

1. **Identify different reproductive populations**, races, and/or stocks which can be managed as separate units.
2. **Estimate population sizes**, exploitation rates, and rates of recruitment.
3. **Develop test models** that attempt to monitor and predict the effects of fishing and other sources of man-induced mortality on shark populations.
4. **Provide real time fishing mortality estimates** of both target and nontarget species.
5. **Encourage international cooperation** on stocks of pelagic sharks that are utilized or taken incidentally in multinational fisheries.

Recommendations for Future Research in Systematics, Geographic Distribution, and Evolutionary Biology of Chondrichthyan Fishes

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Although research on cartilaginous fishes is marginally funded in most parts of the world, important advances in our knowledge of chondrichthyan systematics, geographic distribution, and evolutionary biology have been made during the past few decades. Future research should continue to investigate the major groups but place additional emphasis on the lesser-known orders such as the squaloids, squatinoids, pristiophoroids, heterodontoids, rhinobatoids, myliobatoids, and chimaeroids. An immediate goal should be the publication of volumes on world batoid and chimaeroid fishes. An interim measure would be a faunal list of world chondrichthyans.

Standards

Perhaps the most important long-term recommendation for systematic research on chondrichthyans is support for an international commission to establish standard measurements and counts, and agreement on how these are to be made. It must be recognized that these will vary with different taxonomic groups. Additionally, standards for measurement of taxonomically significant internal and external structures, including chondrocrania, scapular and pelvic girdles, claspers, vertebrae, teeth, dermal denticles, and soft tissues such as spiral valves and gonads must be established. To the greatest extent possible, nomenclatural standards for anatomic terminology, abbreviations and morphologic description (such as size, shape, coloration, marking and thorn patterns), should also be established. Standards for determining and describing stages of sexual maturity, condition of reproductive organs and development of embryonic and fetal stages would be most useful.

Recording Documents

Standard recording documents should be developed and widely disseminated. These should include forms to be used by fishermen, fisheries workers, and fish processors to record needed field information, including species, size, sex, maturity, coloration, markings, environmental parameters, geographic location, capture method, and other data. Other forms for systematists and systematic collections personnel would be used to record standard measurements, counts, and other taxonomically important data. Correctly designed forms, which can extract all the needed information, yet be easily used and universal in their application, are badly needed.

Emphasis should be given to standardizing these forms for international use to serve as documents to support a systematic database, for which international agreement, developmental funding, and support would most likely be needed.

Databases

An international database which accepts and continuously updates field and systematic input must be developed. Priority should also be given to developing databases for systematic collection holdings, host-parasite records, and bibliographic data entries. Laser disc technology could be used for archival purposes.

Consideration should be given to subsidizing the cost of using such databases, to permit access to capable and qualified researchers on limited budgets.

Lists and Announcements

Less formal than databases, and quite suitable for interim or localized information exchange, are lists and announcements, both for information available and for what is needed. Examples of the first might include collection holdings, recent additions to collections, type specimens, and specimens available for loan or exchange. To increase collaboration in obtaining specimens, announcements of forthcoming collecting trips, research vessel cruises, and lists of supportive sport and commercial fishermen should be distributed. Examples of the second might include lists for needed specimens, ''parts'' (jaws, teeth, stomachs, reproductive organs), parasites, photographs or slides, and literature. The *American Elasmobranch Society Newsletter*, the *Chondros* newsletter, the *Report of Japanese Society for Elasmobranch Studies*, and the *Newsletter of Systematic Ichthyology* currently serve as an informal forum for such announcements.

Facilities

Chondrichthyans are the largest fishes, a characteristic which has proven to be one of the greatest setbacks to systematic research. Because of their large size and the great expense associated with collecting, preserving, transporting, and storing specimens, they are often poorly represented in systematic collections.

A review of current research facilities should be undertaken to identify needed updates.

It is not inconceivable that a safe, effective, and practical preservation method using a gaseous, cryogenic, ionic, or other medium could be developed, and research toward this end should be undertaken. Until such a time, however, containers of alcohol or formalin appear to be the only practical and widely used means of preserving chondrichthyan specimens.

Improvements in storage containers and handling systems should be considered. A standardized design to allow interchangeability, repair using standard parts and competitive procurement of large lots, to obtain the lowest possible unit price, should be developed. Several convenient sizes should be considered, including sizes to accommodate large specimens to 20 feet total length. To save floor space in collection rooms, containers should be designed to be stackable, and integral handling systems should be used similar to those common to warehouses, to retrieve the container and transport it to the work area. Containers should be relatively shallow, have broadly rounded corners, built-in sensors for low fluid levels or chemical imbalance, and be fitted with integral lifting baskets. Handling systems should be designed to permit retrieval from both sides, allowing two stacks to be served by a single aisleway.

Work areas should be considered for updating to permit safe and efficient handling of large specimens. Hoists with slings for lifting and turning specimens and monorails to ease movement between workstations are important. Adequate lighting and ventilation should be provided. Floors, tables, and walls should be made of materials which permit hosing down. Industrial drains to handle large quantities of liquids while trapping particulate matter should be installed. Ventilation scrubbers and liquid separators may be required to meet environmental regulations.

Some costly but useful and labor saving technology could include adjustable-height measuring tables with suspended, positionable holders for stereomicroscope heads, ring light magnifiers, cameras or other optical devices. Electronic or electro-optical measurement capabilities, using digital calipers, position indicators, and numeric keypads would permit direct entry of measurements into computerized databases. Properly shielded work areas, with x-ray tubes positioned on gantries, would simplify radiography of large specimens. Programmable, fluoroscopic imaging systems would permit real-time investigation of skeletal and other internal structures. Documentation of especially large specimens could be accomplished using videotape; and archival storage could use laser disc technology.

Standards for nomenclature, description, and cataloguing of fossils should be compatible with those for living chondrichthyans, to the greatest extent possible. Recording techniques and documents should be standardized to permit development of databases that could be queried by geologic strata, era, geographic location, or other fields. Bibliographic databases should be developed and literature archived using laser disc technology.

Development of criteria for biochemical techniques to support systematic study should be undertaken. Karyotype studies, nuclear DNA composition and immunological techniques to determine phylogenetic relationships, have been accomplished on only a relatively few species of chondrichthyans, owing, in part, to the requirement for live specimens, their relatively large size, occasional aggressiveness, and relative inaccessibility. Standard techniques for collecting and processing biochemical samples should be developed for field use by nonbiochemists. Findings should be entered in a database which could be queried according to species or other taxa.

Chondrichthyans are host to a variety of ectoparasites and endoparasites, most of which are rather host specific. As such, they can be excellent indicators of phylogenetic interrelationships. Research efforts should include developing standard techniques for collecting, identifying, and preserving parasites. Field and laboratory input records should be developed to link host, parasite, location, environmental, and other parameters in a database.

Support for the Nonspecialist

There are many examples in which the nonspecialist—the sportsman, commercial fisherman, fishery worker, or scientist from an unrelated field—has made the initial find of a new chondrichthyan species. Their continued involvement should be encouraged and supported. Concise, understandable, and easily used identification guides, in a number of languages, should be developed and made readily available. Suitable low cost specimen containers in a variety of sizes should be developed and made available to fishermen, field researchers and others willing to supply specimens. A scientific ‘‘need list’’ should be published and widely disseminated. Where specimens must be shipped, cooperative agreements among local institutions and agencies, to absorb the burden of packaging and shipping expense, should be established.

Chondrichthyan Research Centers

Because of their unusual storage and handling requirements, and the high cost and physical impracticality of upgrading many existing collection facilities, consideration should be given to support the establishment of a number of regional chondrichthyan research centers. These centers could be funded and operated jointly by government, academic, and private interests. They would provide regional focal points to serve as clearing houses for information and specimen exchange, and to help coordinate research efforts. They would be equipped to provide extensive computer, database, library, archival and training support. They would have well-equipped research facilities with on-site dormitory facilities for visiting scientists. A portion of their construction costs would be amortized by serving as repositories for specimen storage. They would do much to alleviate the often crowded conditions in existing collection facilities by assuming collection management responsibility for the largest, if not all, chondrichthyan specimens.

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